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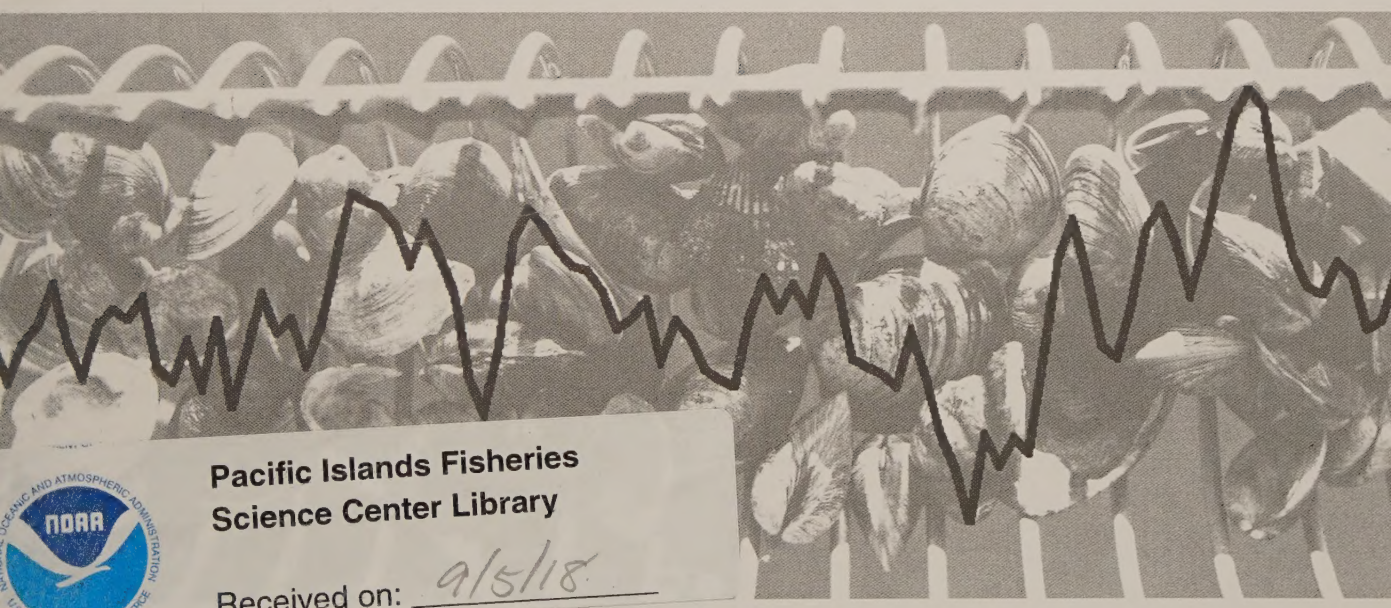

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Bivalves and the North Atlantic Oscillation

Marine Fisheries REVIEW

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Large Shifts in Commercial Landings of Estuarine and Bay Bivalve Mollusks in Northeastern United States after 1980 with Assessment of the Causes — *Clyde L. MacKenzie, Jr.*, and *Mitchell Tarnowski* 1

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Large Shifts in Commercial Landings of Estuarine and Bay Bivalve Mollusks in Northeastern United States after 1980 with Assessment of the Causes

CLYDE L. MACKENZIE, Jr., and MITCHELL TARNOWSKI

Introduction

In U.S estuaries and bays from Maine to North Carolina (Fig. 1), commercial landings and associated abundances of the four major, commercially important bivalve mollusks have experienced large synchronous declines between 1980 and 2005. The bivalves are eastern oysters, *Crassostrea virginica*; northern quahogs, *Mercenaria mercenaria*; softshell clams, *Mya arenaria*; and bay scallops, *Argopecten irradians* spp. Their combined landings declined by 85% (Table 1). The numbers of fishermen who harvested the bivalves declined similarly (Table 2). These downturns have deprived fishermen of their historical livelihoods, and many waterfronts that had once been dedicated to commercial fishing are now dominated by private and tourist housing, restaurants, and sporting vessels. Once common seasonal foods for coastal people, these bivalves have become far less available in consumer markets (authors' observations).

The bivalve declines are in contrast to the previous three decades (1950–80), when the combined landings of the same bivalves were much higher and the trend in each of their annual landings was nearly level, decade by decade. However, the landings of northern quahogs in Connecticut have risen sharply. The landings of American lobsters, *Homarus americanus*, have also increased sharply in Maine, but have fallen precipitously (from 40% to 98%) from southern Massachusetts to New Jersey (see Appendix). Additionally, groups of marine and land animals have also experienced large abundance changes since the early 1980's. For example, the landings of the 14 most important commercial marine groundfish caught on ocean bottoms off the U.S. northeastern coast fell by about 78% between 1980 and 2013, or almost as much as the molluscan landings (NOAA Annual Commercial Fishery Landings Statistics[1]).

Our assessment of the declines in bivalve landings was undertaken to pursue one of the primary missions of NOAA's National Marine Fisheries Service: to understand how climate changes modify ecosystems and thus abundances and landings of commercial marine species. A major change to the bivalve habitats occurred when the North Atlantic Oscillation (NAO)

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[1]NMFS Annual Landings Statistics available online at https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index.

ABSTRACT—Between 1980 and 2010, documented commercial landings of the four most commercially-important bivalve mollusks have declined sharply in U.S. estuaries and bays from Maine to North Carolina. The numbers of shellfishermen have declined accordingly. Landings of the following species have declined: eastern oysters, Crassostrea virginica, *by 93%; northern quahogs,* Mercenaria mercenaria, *by 62%; softshell clams,* Mya arenaria, *by 66%; northern bay scallops,* Argopecten irradians irradians, *by 93%; and southern bay scallops,* A. i. concentricus, *by 91%. Their combined landings fell by an estimated 85%. In the previous three decades, 1950–80, annual landings of the same species did not decline.*

The declines in landings of the bivalve mollusks were a consequence of declines in their abundances which was due to falling juvenile recruitments. The declines took place after the molluscan environments changed adversely for the bivalves as the North Atlantic Oscillation index switched its phase from negative to positive in about 1982 and usually remained there until 2003. Winters then became substantially warmer while the other seasons were also warmer, but less so. The temperature increases in winter and spring probably forced weight losses in the adult mollusks, and, consequently, they spawned fewer eggs. The increased temperature also allowed heavy feeding by pelagic copepods on phytoplankton, which left too little food available for the adult shellfish and their larvae to produce good seed recruitments. Also, predation on the juvenile recruits may have increased, which precipitated the declines.

From Long Island Sound, N.Y., through Chesapeake Bay, Md., warmer waters allowed diseases to kill many adult oysters. In some waters, higher temperatures increased the negative effects of eutrophication, and in other waters the loss of eelgrass, Zostera marina, *probably contributed to degradation of habitats. This paper also discusses the role that crustaceans, i.e., pelagic copepods, shrimps, and crabs, play in the productivity of bivalve mollusk stocks. Predation by penaeid shrimp on tiny bivalve recruits is suggested as an important factor that controls bivalve abundances. The common perception that bivalve landings declined due to overfishing is reconsidered, because separate environmental factors have had a much larger effect upon their productivity.*

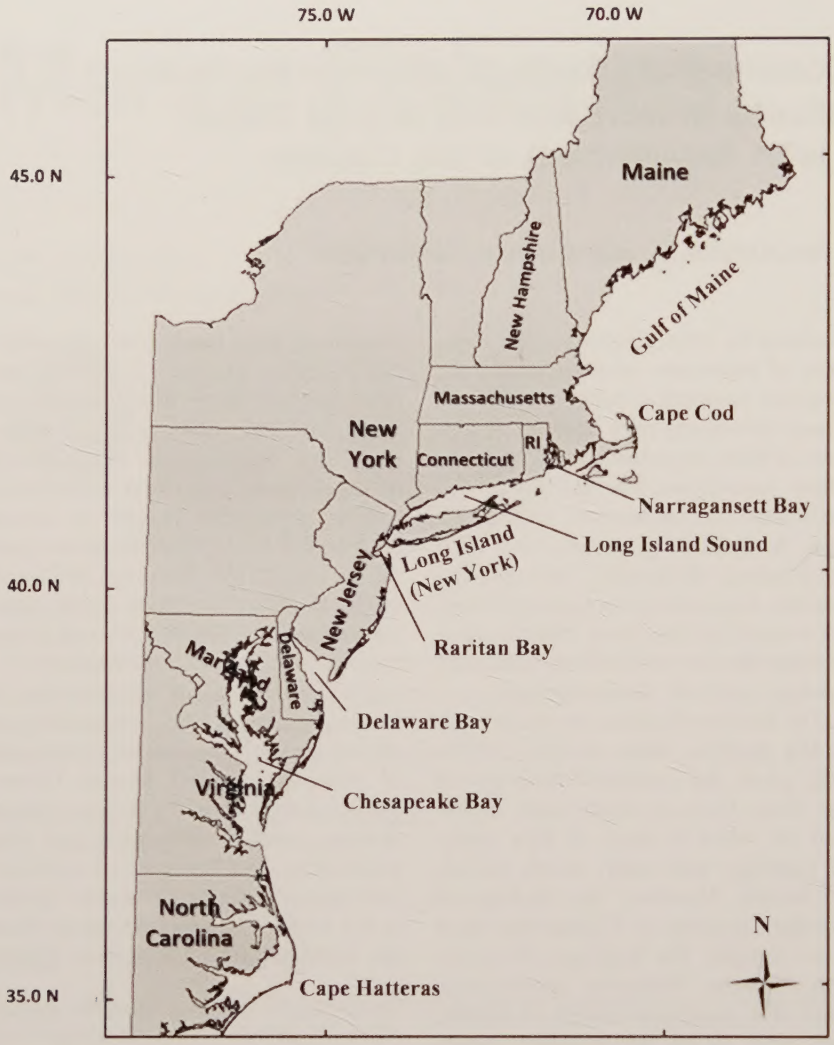

Figure 1.—The United States coastline, Maine to North Carolina, showing states and some major water bodies.

Table 1.—Some overall changes in animal and plant life in the U. S. and some other locations while the NAO was in a positive mode between 1982 and 2003 and when temperatures were higher especially in winter.

Marine Life

1. Huge decline (78%) of 14 most important species of groundfish landed off U. S. east coast between 1980 and 2005.[1]
2. Huge losses of Atlantic surfclams in New Jersey state waters, softshell clams in Maryland and New Jersey, and loss of lobsters south and west of Cape Cod, Mass., and Long Island (see text).
3. Huge decline in oyster landings in Delaware and Chesapeake Bays and also landings declines in quahogs, softshell clams and bay scallops (see text).
4. Large decline in groundfish and a concurrent increase in crustaceans in Narragansett Bay, Maine coastal waters[1], Gulf of St. Lawrence, Canada (Jenkins et al., 1997).
5. Large increases in lobsters in Maine, and northern quahogs in Connecticut.[1]
6. Some losses of eelgrass (Fonseca and Uhrin, 2009).

Land Animals

1. Large increases in land animals (mammals) (Von Drehle, 2013)
2. Large increases in cormorants in North America and western Europe (www.epa.gov/med/grosseile_site/indicators/cormorants.html, and Kohl, 2010).
3. Northward movements of birds in North America (Niven et al., 2013).
4. Decrease in song birds in the U.S. (www.nativesongbirds.org/Help_Songbird.html.

[1]NMFS annual commercial landings data found in U.S. Fisheries Statistics and Fisheries of the United States.

index switched from negative (during about 1950 to 1980 when winter temperatures were relatively cool) to positive resulting in warmer winter temperatures from about 1982 until about 2003.

We suggest that this climate shift affected the bivalves and their associated biota enough to cause the declines. We have used research results from extensive habitat studies in Narragansett Bay, R.I., and in Europe, especially the Wadden Sea, where salinities and temperatures are similar to the northeastern U.S. coast. Collectively, these studies show that body weights of the bivalves, their nutrition, timing of spawning, and perhaps mortalities from predation were affected sufficiently to force the declines.

Other factors relating to the overall declines were eutrophication, decline in attachment sites for bivalve larvae, and weak consumer demand. Our assessment applies to the bivalves in all locations along this coast. This review is by no means comprehensive but it is sufficient to provide an overview of the salient factors that contributed to the declines.

Our findings are mainly correlative in kind because the information we collected and considered does not cover all the locations. The importance of calanoid copepod feeding on phytoplankton is mostly from the waters of Narragansett Bay, R.I., and penaeid shrimp and green crab, *Carcinus maenas*, predation on juvenile bivalves is mostly from the Netherlands. Our past studies on predation on oysters (MacKenzie, 1981), quahogs (MacKenzie et al., 2002), bay scallops (MacKenzie and Lind, 2013), and surf clams (MacKenzie et al., 1985) illustrated the same rapid destruction of bivalve recruits that European scientists documented. This will be discussed in a later section on European observations. We have assumed that this information roughly reflects conditions in most of the estuaries and bays of the northeast. At least one of the authors has personally visited all the major production beds from Maine to North Carolina, while accompanied by state

personnel and local shellfishermen. Nevertheless, our conclusions are to be considered as suggestions because they are based on correlations; they can serve to drive future research. The common perception that the bivalve landings have declined mainly due to only overfishing will be reconsidered here because separate environmental factors are identified that have had much larger effects. We have not included bivalves that were produced by aquaculture (larvae reared in hatcheries) in this study.

We have included observations relating to reproduction of bivalves reported in various international publications by scientists in Europe, mainly the Netherlands, because some aspects are more extensive than those reported in the United States. The effects of predators on European bivalves probably are similar to those on the bivalves in the northeastern United States because some species are the same or closely related, such as the softshell clam, the shrimp, *Crangon* spp., and the green crab. Salinities are also similar.

Table 2.—Comparison of the numbers of molluscan and lobster fishermen along the U. S. east coast, Massachusetts to Virginia, in early 1980's and early 2000's.

Species	Location	Early 1980's	early 2000's	% Change
Oyster				
Market	Connecticut	36	6	-83%
Seed	Connecticut	45	3	-93%
Seed	New Jersey	70	45	-36%
Market	Maryland	1,246	81	-93%
	Subtotal	1,397	135	-90%
Quahog				
	Great South Bay	1,500	6	-99%
	Connecticut	15	120	+700%
	Raritan Bay, NY, NJ	180	40	-78%
	Barnegat Bay	30	5	-83%
	Chincoteague Bay, MD	30	0	-100%
	Subtotal	1,755	171	-90%
Softshell clam				
	Boston, MA	169	0	-100%
	Chatham, MA	200	0	-100%
	Raritan Bay, NJ	18	0	-100%
	Chesapeake Bay, MD	225	0	-100%
	Subtotal	612	0	-100%
Bay scallop				
	Edgartown, MA	80	25	-69%
	Nantucket, MA	310	60	-81%
	Chatham, MA	300	0	-100%
	Peconic Bay, NY	300	20	-93%
	Subtotal	990	105	-89%
Atlantic surfclam				
	New Jersey State waters	80	0	-100%
	Subtotal	80	0	-100%
Lobster				
	Connecticut Western to Middle Long Island Sound	279	48	-83%
	Raritan Bay & Atlantic Ocean	56	0	-100%
	Subtotal	335	48	-86%
Total		5,169	459	-91%

Data Collections

Data on annual landings of bivalve mollusks were obtained from compilations by NMFS under Annual Landings Statistics[1] and various states since 1950. Recordings of shellfish landings began in 1880, both as a state and federal responsibility (Sutherlund and Koplin, 1997). Data were collected from mandatory and voluntary reporting systems, including logbooks submitted by commercial companies, and from our interviews of town and state shellfish constables, seafood dealers, and our personal observations in the bays.

Principal data consist of species landed, pounds of meat, and landed values in each state. Landings data for bivalves presented herein are in bushels (1 bu equals 35 l) of whole bivalves, but whole weights of American lobsters and finfish are listed. The meat-to-bushels ratio was calculated by using conversion factors listed under Statistical Survey Procedures in the NMFS Statistical Digests (Fishery Statistics of the United States, 1970). Conversion factors for each mollusk will be listed in the landings tables.

Factors affecting the collection of landings data are under-reporting and not reporting due to confidentiality. NMFS has taken care to ensure that the data are accurate, but voluntary reporting is subject to carelessness and bias, and all possible contributors may not be identified or reported. The data are sufficiently reliable to show the trends in annual landings (Sutherland and Koplin, 1997).

Data for numbers of fishermen were collected from state records, interviews with fishermen, state and town shellfish constables, local biologists, and our personal observations. The numbers of fishermen listed represent those harvesting on the beds rather than the numbers of fishing licenses that were issued by a town or state. Data from the fisheries in every location could not be included. Trends in fishery landings described herein correspond mostly to the changing abundances of stocks, but market demand by consumers also plays a role. When demand is weak and prices are low, fishing efforts and landings commonly are less than when demand and prices are higher.

In some waters we sampled the species of pelagic copepods and ctenophores and recorded their numbers. To do so, we towed a net behind a boat for 10 min at each site. The net had an opening 19.8 cm in diameter; the mesh openings in the net were 335 microns. The mesh size was too large to retain bivalve larvae.

North Atlantic Oscillation

In the North Atlantic Ocean and surrounding continents, the index shifts of the North Atlantic Oscillation (NAO) (Fig. 2) have a dominant influence over climate variability (Hurrell, 1995) and, consequently, over ecosystems and fisheries (Ottersen et al., 2001). The state of the index affects the timing of the species' reproduction, bivalve phytoplankton foods, predator-prey relationships, and ultimately their abundances. Each estuary and bay has

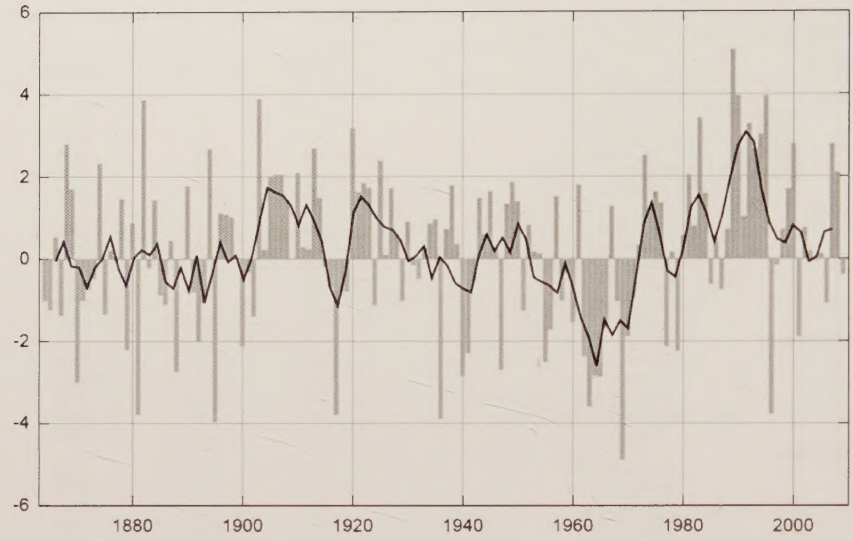

Figure 2.—Trend of the North Atlantic Oscillation index, 1865–2010; black line represents 5 year moving average. Source: NAO Index Data provided by the Climate Analysis Section, NCAR, Boulder, NSA, Hurrell (2003). Updated regularly. Accessed 08 Oct. 2017, Wikipedia.

tightly coupled ecosystems that are strongly influenced by the NAO (Kirby et al., 2009).

The NAO relates to the shifting in the atmospheric air pressure at sea level between the high pressure zone around the Azores, west of Portugal, and the low pressure zone at Iceland and Greenland. The NAO affects temperature, wind, and precipitation, especially in winter and early spring when the atmosphere is more active than in other seasons in the North Atlantic Ocean between approximately lat. 40°N and 60°N (in North America, from mid-New Jersey to northern Newfoundland; in Europe, from mid-Portugal to lower Norway and Sweden (Hurrell, 1995)).

When the air pressure difference is small, the NAO index phase is negative, and winters are relatively cold and dry. When in its positive phase, westerly winds are stronger than otherwise, air and seawater are warmer, most noticeably in winter, and also precipitation is heavier. Winter is the season in which the NAO has its greatest influence on bivalves and other biota (Marshall et al., 2001), and large variations in the NAO can occur among winters and also within each of the seasons (Hurrell and Deser, 2009). Thus, during the 1950's to early 1980's, annual bivalve recruitments by year commonly ranged from high to low, despite what appeared to be a consistently negative NAO index phase when weekly indices were averaged for a full year.

Early studies of the NAO dealt with its physical aspects (Hurrell, 1995), but investigative work since the mid-1980's has been focusing on how its contrasting negative and positive indices affect marine and terrestrial populations in the United States (Hurrel et al., 2003) and Europe (Stenseth et al., 2002). Studies have shown that when marine waters warm, some fish migrate northward to cooler habitats; if fish were to remain in place, they could perish when temperatures rose above the extremes they can tolerate (Murawski, 1993; Beaugrand et al., 2002). In addition, the diseases MSX and Dermo have shifted much farther north from Chesapeake and Delaware Bays to new areas, for example into Connecticut waters where they killed many oysters (Ford, 1996; Cook et al., 1998).

In the early 1980's, the NAO index switched to its positive phase and the rising temperature affected many groups of marine plants and animals in the United States and Europe (Ottersen et al., 2001). The groups included phytoplankton (Irigolen et al., 2000); calanoid copepods and other zooplankton (Ottersen et al., 2001; Beaugrand et al., 2002; Oviatt, 2004); jellyfish (Lynam et al., 2004; Purcell and Dekker, 2005); bivalve diseases (Soniat et al., 2009; Soniat et al., 2012a; Bushek et al., 2012); blue crabs, *Callinectes sapidus* (Sanchez-Rubio et al., 2011); sea turtles (Baez et al., 2011); and the compositions of biotic assemblages along with recruitments, abundances, and growth of juvenile marine fish during their estuarine and bay residences (Dippner, 1997; Tunberg and Nelson, 1998; Ottersen et al., 2001; Parsons and Lear, 2001; Attrill and Power, 2002; Brander and Mohn, 2004; Henderson and Seaby, 2005; Aburto-Oropeza et al., 2010). The increase in winter temperature lessened cold stress and thus reduced the mortality of many animals, including juvenile Atlantic croakers, *Micropogonias undulatus*, in Barnegat Bay, N.J. (Hare and Able, 2006), and animals on land (Straile and Stenseth, 2007).

The NAO index might be a good predictor of interannual variability in animals and plants because of its effects on them in the early spring (Hurrell, 1995; Hurrell and Deser, 2009). Use of this index could help observers make predictions of interannual variability in the recruitment magnitudes of juveniles and hence population sizes (Straile and Stenseth, 2007). Stenseth et al. (2002) believe, though, that making firm predictions about the effects of the positive NAO index and its higher temperatures, along with its stronger winds and heavier rainfall, on abundances of biota should be tenuously considered. Nevertheless, if the role of the NAO is not considered, incorrect conclusions can be drawn regarding the relative contributions of anthropogenic vs. naturally occurring disturbances in regulating marine biological systems (Hurrell and Van Loon, 1997; Ottersen et al., 2001).

Since the Industrial Age began in about the mid-1850's, the earth's temperature has risen by about 0.7°C (Bindoff et al., 2007). After about 1980, the North Atlantic Oscillation (NAO) in the United States has substantially augmented this rise, especially in winter, when it shifted to and usually remained in its positive phase. In Narragansett Bay, Mass., mostly in the warm years of the late 1980's and early 1990's, winter mean temperatures were 1°–3°C above earlier means; they rose about 2°C from about 1970 to 1994 (Oviatt, 2004). In Chesapeake Bay waters, winter temperatures rose from 0.8° to 1.1°C from 1950 to 2002; they correlated well with sea surface and surface air temperatures (Preston, 2004). In European estuaries, the strongest rises also occurred in winter and spring; water temperatures were about 3°C above the earlier winter means, +1°C to +2°C above spring means; 0°C to 1.5°C during summer; and <1°C above means during autumn (Beukema, 1992; Kirby et al., 2008).

Historical Harvesting of Bivalve Mollusks

Many northeast U.S. coastal region communities had relied on farming, shellfishing, and finfishing for sustenance and economic benefit from prehistoric times to at least the 1940's (Ingersoll, 1881, 1887; Kochiss, 1974; MacKenzie, 1992, 1996). In the early 1900's, the various coastal states assumed management of their shellfisheries. The states established seasons during which the bivalves could be harvested on public beds, permitted only certain gears for harvesting, and restricted the sizes and quantities to be taken by day and season. The restrictions were applied to allow the stocks to endure for an entire open season and to be sustained so the fisheries could remain viable year after year. Some grounds became available for private leasing to allow individuals to culture oysters.

The following four bivalve species comprise the majority of shellfish landings along the northeast U.S. coast. Over time, the eastern oyster was the dominant bivalve landed, and its fishery existed on a large commercial scale throughout the 1800's, 1900's, and into the 2000's. Following in prominence has been the northern quahog whose fishery provided employment for several thousand workers along the U.S. coast from the late 1800's through the 1930's (MacKenzie et al., 2002). Commercial quantities of softshell clams have been landed in every state from Maine through Maryland. Maine usually has been the major producer, but Maryland produced about as many as Maine from the late 1950's into the early 1990's.[1] Northern bay scallops occur in a narrow north-to-south geographic range from the east coast of Cape Cod, Mass., to southern Long Island, N.Y., a distance of 160 km (90 mi). The east-west distance is 340 km (210 mi). Scallops have been harvested in Massachusetts, Rhode Island, Connecticut, and New York. The southern bay scallop once occurred in commercial quantities in several states from New Jersey through North Carolina, and an active fishery remains in North Carolina.

After World War II, many alternate employment opportunities became available (McCay and Jenks, 1997). As the human population increased, this region has become an amalgam of large urbanized centers, suburban sprawl, and recreational facilities that have overwhelmed the relevance of bivalve harvesting and also caused some degradation to estuarine habitats. Relatively few people in the former fishing towns now actively catch bivalves for commerce or have the vocational skills related to fishing and the associated knowledge, beliefs, and behaviors that accompany them. The original waterfronts remain, but more expensive housing, tourist-related and upper-scale retail shops and restaurants, and recreational boats have replaced most fishing sheds and commercial boats.

After 1980, the numbers of fishermen who harvest the coastal bivalves and lobsters from Cape Cod, Mass., to Virginia began to decline substantially (Table 2). The quantities of bivalves in the beds were falling to such an extent that many fishermen found it difficult to earn a living from harvesting them, and they abandoned the industry. Some moved to jobs in other types of fisheries, but most found different types of employment; and parents have discouraged their children from entering commercial shellfishing as an occupation. By the early 2000's, the overall declines in shellfishermen averaged 89% (range, 43–100%) for the various species.

Many who traditionally would have gone into the fisheries (because money could be made and training for the work was minimal) now seek other employment because abundances of bivalves and fish have become relatively low, working hours can be long, financial security is lacking, and incomes are often uncertain and irregular. They also lack the benefits of paid sick leave, vacations, and retirement income. Reduced bivalve fisheries now remain in many locations, based on persistent stocks and market demand for the bivalves.

Historical Landings and the NAO

Oysters

A sketch of the history of oyster landings in the northeastern U.S. from their recorded beginning in the last quarter of the 1800's to the current time will include how they were affected by the NAO, habitat degradation, "overharvesting," bacterial contamination, and market demand. Oyster production was rising to its historical peak during 1885 to 1905 (Ingersoll, 1881; Robertson, 1923; Lyles, 1969), with most of the landings from Chesapeake Bay, Delaware Bay, and Long Island Sound.

In examining the index cycles of the NAO during the 140 years from 1865 to 2005 (Hurrell, 1995; Hurrell et al., 2003; Hurrell and Deser, 2009) (Fig. 2), we note that swings in oyster landings somewhat correspond to those cycles (Table 3). When the oyster industry was developing and increasing in size from about 1865 to 1902, the NAO index usually was

Table 3.—General modes of the North Atlantic Oscillation (mean winter), negative modes compared with positive modes (Hurrell et al., 2003) (See Fig. 4), and oyster landings during 5 time periods, 1865 to 2010 (Lyles, 1969; NOAA Fisheries Landings Statistics).

Time period	Years	NAO mode	Oyster landings trends
1865–1902	37	Negative	Increasing
1903–1930	27	Positive	Poor
1931–1978	47	Negative	Level
1979–2002	23	Positive	Decreasing
2003–2010	8	Neutral	Slightly increasing

Table 4.—Landings of oysters (bushels x 1,000)[1] by State, 1950–2010.[2]

Year	MA	RI	CT	NY	NJ	DE	MD	VA	NC	Total
1950	30.4	131.7	464.6	1,171.6	1,207.0	356.8	2,824.7	3,109.5	424.20	9,720.5
1955	22.3	5.7	53.0	180.5	867.4	548.4	3,386.6	4,391.1	132.9	9,568.0
1960	14.7	3.5	46.9	108.0	27.8	29.4	2,307.8	3,068.1	221.1	5,827.4
1965	7.8	1.6	35.1	26.6	87.2	5.7	1,690.2	2,513.7	157.0	5,524.9
1970	7.8	1.0	16.3	69.2	112.9	36.0	3,259.8	1,608.7	69.5	5,182.2
1975	8.1	0	70.0	280.9	162.0	32.5	3,216.1	1,247.4	77.2	5,094.3
1980	39.4	0	90.3	171.2	126.0	83.7	2,930.3	1,569.3	131.5	5,146.7
1985	11.7	0	112.3	39.8	48.9	6.6	1,685.7	904.7	99.2	2,908.8
1990	4.2	0	380.1	106.7	83.4	0	565.2	326.6	59.8	1,525.7
1995	--[3]	1.1	431.2	47.0	26.0	3.1	234.9	79.6	40.1	863.1
2000	--	13.6	81.0	9.9	33.7	13.0	464.4	32.6	37.0	687.2
2005	15.0	8.0	--	--	26.9	14.0	144.0	3.0	68.7	--
2010	31.0	9.0	--	9.0	92.0	12.0	84.0	79.0	189.2	--

[1]A bushel contains about 7.7 lb (3.5 kg) of oyster meats in Connecticut and New York, and 5.1 lb (2.3 kg) of meats in Chesapeake Bay (Maryland and Virginia).
[2]NMFS annual commercial landings data found in U.S. Fisheries Statistics and Fisheries of the United States.
[3]Unknown data.

in its negative phase. But when the landings were declining from 1903 to 1930, the NAO index usually was in its positive phase. From 1931 to 1972, when the index usually was in a negative phase, annual oyster landings were relatively constant over time. In Chesapeake Bay oyster landings were somewhat level by year with no trend from about 1931 to 1959 and landings averaged about 6.6 million bu/yr (Lyles, 1969).

We point out, though, that these recorded landings are not necessarily an accurate reflection of the quantities that were available to harvest on the beds: the magnitudes of harvesting efforts by fishermen and the available consumer markets have large roles in determining annual production. Oyster landings in Long Island Sound and Delaware Bay had begun to decline during the early 1950's due to a severe storm in 1950, especially in Connecticut. From 1979 to 2002, the NAO index was in its positive phase and oyster landings declined. Then, from 2003 to 2010, the phase was negative or in a neutral phase and oyster landings in Chesapeake Bay were somewhat increasing.

Several factors contributed to the decline in oyster landings after 1900. During the last quarter of the 1800's, heavy oyster sets were routine and the oyster industry was flourishing and increasing in size while meeting the food demands of the growing human population. Subsequently, however, the NAO index was in its positive phase and between about 1900 and 1925, Connecticut rarely had a good set and its oyster landings declined (Robertson, 1923; Loosanoff, 1966). We suggest that the poor oyster recruitments may have also occurred in the Chesapeake and Delaware Bays.

The loss of shell as a habitat component due to harvesting was another negative factor. Moore (1911) stated that in Delaware Bay (Delaware), so many shells and oysters were removed by commercial dredging boats that sections of former seed beds were left with nearly bare sand and little substrate for oyster larval settlement. Ford (1997) later described how the seed beds in the New Jersey section of Delaware Bay were partially stripped of shells by commercial dredge boats. This was followed by lower seed production from the beds.

A third factor was the falling consumer demand for oysters during the early decades of the 1900's. Beef, pork, and later finfish became much more available for consumers who gradually switched to them for food. The switch was accelerated as oyster sanitation scares among consumers arose in the early 1900's. Flush toilets were coming into widespread use, and some untreated human wastes were pouring directly into waters, contaminating oysters (Turner, 1910; Churchill, 1911; Bundesen, 1925). The contaminates included bacteria (cholera, *Vibrio cholera*; typhoid, *Salmonella typhosa*). Newspaper reports about human illnesses resulting from eating oysters caused some people to avoid eating them, especially raw (MacKenzie, 1996). Various states were forced to leave large quantities of market-sized oysters on their beds for future seasons. The last year of large oyster production in Virginia was 1907 (Lee, 1914). In 1907, fearing the oyster industry might collapse, the private oyster growers formed the Oyster Growers and Dealers Association to publicize the benefits of eating oysters (Anonymous, 1908). Still, the oyster landings continued to fall (Anonymous, 1911).

In sum, the steep fall in oyster landings after 1900, was not simply a consequence of fishermen overharvesting oysters on the beds, as many scientists, including we authors, have routinely stated. There appeared to be consistently poor seed production during this period that was related to unfavorable climate conditions associated with the positive NAO index. Bottom shell habitat depletion from harvesting activity and silt accumulations on beds were also a factor in low recruitment. In addition, consumer demand for oysters fell sharply due to health concerns and a change in preference to meats and finfish.

1950–1980: No Trends in Bivalve Landings

From 1950 to 1980, there was no trend in total annual landings of each of the bivalve species (all states combined), although there was considerable interannual variability in annual bay scallop landings. The only exception was the oyster landings between 1950 and 1965: they fell from 9.6–9.7 million bu to about 5.0–5.5 million bu, coincident with the initial epizootic mortalities in Delaware and Chesa-

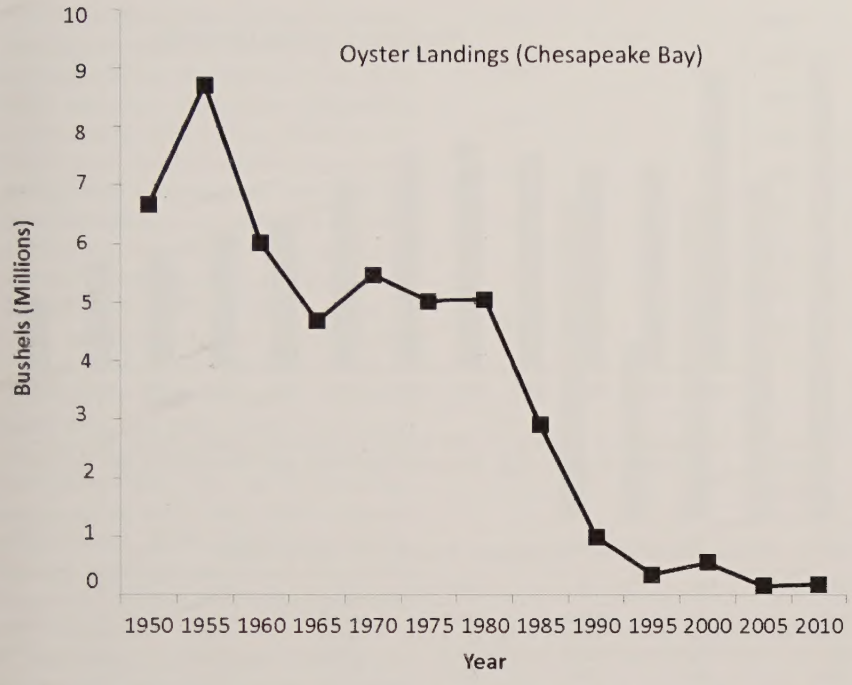

Figure 3.—Landings of oysters in Chesapeake Bay, 1950–2010. Source: U.S. Fisheries Statistics and Fisheries of the United States.

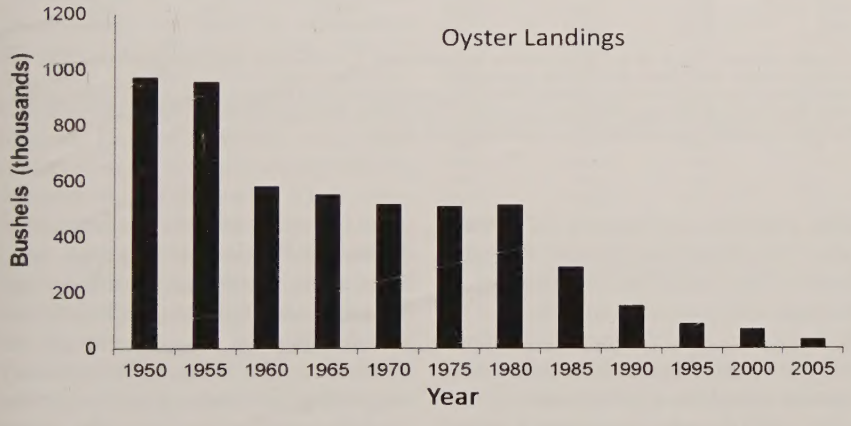

Figure 4.—Landings of oysters from Connecticut, New Jersey, Delaware, and Maryland–Virginia, 1980 to 2005. Source: U.S. Fisheries Statistics and Fisheries of the United States.

peake Bays. They remained at about this latter quantity from then until 1980 (Table 4).

Oyster landings were documented in every state from Massachusetts to North Carolina, with the largest landings from Maryland and Virginia (Chesapeake Bay) (Fig. 3), where their joint landings comprised nearly 80% of the total. From 1950 to 1980, Maryland's landings were 1.7–3.4 million bu. Virginia's landings from 1950 to 1965 were 2.5–4.4 million bu, dropping to from 1.25 to 1.6 million bu from 1970 to 1980 (Fig. 4). The next leading states in oyster production were New York, New Jersey, and North Carolina. Connecticut, Delaware, Massachusetts, and Rhode Island also produced substantial quantities of oysters. From 1950 to 1980, the oyster landings in Massachusetts ranged from 7,840 to 39,400 bu; landings from Rhode Island were smaller (Table 4).

The average annual landings of quahogs from the states with the highest landings were 1,250,000 bu/yr between 1950 and 1980 (Fig. 5). New York, with an average of 496,000 bu produced 43% of the total. Landings in New Jersey averaged about 210,000 bu/yr; Rhode Island, 216,000 bu/yr; Virginia, 114,000 bu/yr; and Massachusetts 113,000 bu/yr (Table 5).

Softshell clam landings from Maine to Maryland averaged 680,000 bu/yr from 1950 to 1980. Maine produced about 295,400 bu/yr, or about 43% of the total from all states (Fig. 6; Table 6). In 1960, 1965, and 1970, Maryland's annual average of 538,000 bu was 2.5 times higher than Maine's landings of 206,600 bu, but Maryland's landing fell considerably afterward in part due to the effects of Tropical Storm Agnes in 1972. The remaining states with substantial landings were Massachusetts with an annual average of 92,000 bu, New Jersey with 13,360 bu, Rhode Island with 9,300 bu, and New York with 7,040 (Table 6).

The average annual landings of northern bay scallops in Massachusetts, New York, Rhode Island, and Connecticut were between 290,000 and 300,000 bu (Fig. 7) (Table7), from the 1950's to almost the mid-1980's. Massachusetts produced about 54% of this total, averaging 160,000 annually with a range between 74,220 to 225,480 bu. In 1950, New York's bay scallop landings were 4,500 bu, but in 1962 they had increased to 165,000 bu. This was the state's best year in scallop landings, and they have declined every year since then. Rhode Island bay scallop landings were relatively small; some scallops were landed in some years of the 1950's, 1960's, and 1970's, but in various years there were no landings; in 1978 there was an unusually large stock and 75,000 bu were landed. Un-

til the mid-1960's, a bay scallop fishery was active in Connecticut. From 1953 to 1965 Connecticut's annual landings of bay scallops went from a high of 70,000 bu down to 2,000 bu, after which the scallops became scarce and the fishery ceased to exist.

1980–2010: Downward Trends in Bivalve Landings

After about 1980, the trend in landings of each bivalve mollusk was downward in most areas of the northeastern states. Annual total oyster landings fell sharply, to about 2.9 million bu in 1985, 1.5 million bu in 1990, 0.7 million bu in 2000, 0.28 million bu in 2005, and about 0.5 million bu in 2010. From 1980 to 2005, overall oyster landings declined by about 94% (Fig. 3, 4; Table 4).

Annual northern quahog landings fell at a slower rate than did the oyster landings. By 2005, New York's landings were 135,000 bu, a decline of about 75% since about 1980. By then, New Jersey landings were about 55% of the total from 1950 to 1975, but they rose after 1990 and remained at about that level. By 2005, landings declines in some other states compared with those from 1950 to 1975 were: Rhode Island, 26%; Virginia, 13%; and Massachusetts, 43%. From 1975 to 2005, the overall decline in total quahog landings from all these states was about 62% (Fig. 5, 8; Table 5).

After 1980, total landings of softshell clams from all states declined steadily (Fig. 6), and by 2000–05 they had fallen by 66% of the 1950–80 annual totals. Maine's landings had fallen by about 20%, while Maryland's landings were down by 97%, and they were almost nonexistent. In New Jersey, softshell clam landings also became nonexistent. Yet the landings in Massachusetts and Rhode Island did not decline (Table 6). Softshell clam landings in Maine totaled 152,300 bu in 2000 and 138,000 bu in 2010. The Maine landings declined mainly because state officials imposed closures of clam beds due to outbreaks of PSP (red tide), caused by the toxic dinoflagellate *Alexandrium tamarense* and high numbers of bacteria in waters where the clams were present. PSP and bacteria can cause serious illnesses to humans who consume the clams. The bed closures were frequent in summer when consumer demand and clam harvesting would be at their peaks.

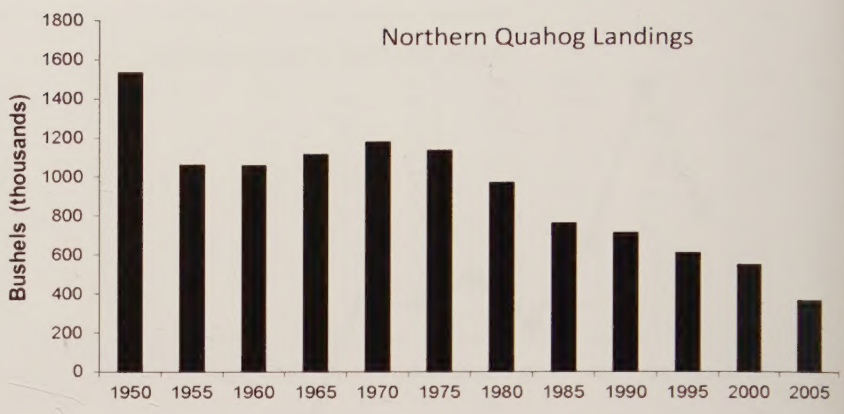

Figure 5.—Landings of quahogs in the major production states, except for Connecticut, 1950–2005. Source: U.S. Fisheries Statistics and Fisheries of the United States.

Table 5.—Landings (bushels x 1,000)[1] of quahogs by the states with largest landings.[2]

Year	MA	RI	NY[3]	NJ	VA	Total
1950	167.8	185.0	643.0	423.0	115.0	1,534.5
1955	88.3	418.3	221.4	260.0	74.0	1,062.0
1960	117.0	267.0	324.0	212.6	138.4	1,059.0
1965	88.3	169.0	495.6	156.1	207.3	2,982.0
1970	104.8	90.0	658.8	214.6	110.8	1,179.0
1975	92.5	93.3	722.0	135.0	90.7	1,133.8
1980	133.2	289.8	412.3	70.4	62.8	968.4
1985	114.3	345.4	156.4	86.3	59.8	762.1
1990	91.7	209.6	205.3	103.1	129.9	739.5
1995	83.3	108.6	219.0	118.8	78.7	608.4
2000	62.5	117.0	196.0	135.0	37.0	547.5
2005	37.2	53.5	134.7	154.3	16.0	395.7
2010	75.0	50.0	117.0	127.6	12.7	382.3

[1]A bushel contains 11 lb (5 kg) of quahog meats in Massachusetts; 12 lb (5.4 kg) in Rhode Island and New York; 10 lb (4.5 kg) of meat in New Jersey; and 8 lb (3.6 kg) in Virginia.
[2]NMFS annual commercial landings data found in U.S. Fisheries Statistics and Fisheries of the United States.
[3]New Jersey landings rose after 1980 because a large bed of quahogs was discovered then in Sandy Hook Bay. Fishermen harvested large quantities from it (MacKenzie et al., 2006).

In 1980, the total annual landings of bay scallops in the region from Massachusetts to Long Island, N.Y., were 297,300 bu, but they fell to 44,200 bu by 1990, and 600 bu in 2000. In 2010, the landings rose slightly to 21,400 bu; most landings were from Nantucket and Martha's Vineyard, Mass. (Table 7; Fig. 7, 9).

Landings of Oysters and Quahogs Rise in Connecticut

In contrast with the other northeastern states, oyster landings in Connecticut rose substantially. From 1955 through 1970, annual landings were from about 16,000 to 58,000 bu, but by 1995 landings were 430,000 bu. The reasons for the increase are attributed to the commercial industry controlling two main oyster predators, starfish, *Asterias forbesi*, and the oyster drills, *Urosalpinx cinerea* and *Eupleura caudata*, and spreading much larger quantities of shells to be used as cultch for setting oyster larvae (MacKenzie, 1981). During the mid-1990's, the disease MSX, *Haplosporidium nelsoni*, infected the oysters, and they died in large numbers. The landings dropped to about 80,000 bu by 2007. Connecticut's landings, thereafter, though substantial in volume, have not been documented.

Quahog landings averaged about 12,000 bu/yr from the 1920's to the

1970's. In those years just a few boats, usually employed for oystering, sought quahogs during the spring when their main activities were slow. Beginning in the early 1990's, the quahogs became much more abundant. Fishermen found large quantities of seed and littleneck quahogs on hundreds of acres of bottoms, in waters 3–12 m deep that extended from Norwalk to New Haven. The quahogs had not been present in such quantities before. Connecticut's annual landings of quahogs began to rise sharply as more boats, including those that had been used for lobstering in Long Island Sound, joined the harvesting fleet after the lobsters became scarce during the 2000's (Pearce and Balcom, 2005). During the 1980's, quahog landings increased to 46,000 bu/yr; during the 1990's they averaged 125,000 bu/yr.

Beginning in the early 2000's, the quahogs became even more abundant; they averaged 334,000 bu/yr; and there were 467,000 bu in 2005 (U.S. Fishery Statistics and Fisheries of the United States) (Fig. 8, 10). We suggest that the quahogs increased in abundance because juvenile rock crabs, *Cancer irroratus*, a primary predator of juvenile quahogs, declined sharply in numbers in 1999. Adult rock crabs had occupied deep bottoms along with the lobsters during summers. They came into relatively shallow waters, 3–7 m deep, during winter, mated, and in the spring released their larvae. The larvae settled in the same shallow waters and fed on invertebrates, including the juvenile quahogs. Most rock crabs died when the lobsters also died in Long Island Sound during the warm months in 1999, owing to stressful environmental conditions (low oxygen concentrations and release of sulfides and ammonium from the sediments) (Pearce and Balcom, 2005). The heavy predation by the juvenile crabs on the quahogs probably then ended. More research is needed to confirm this hypothesis.

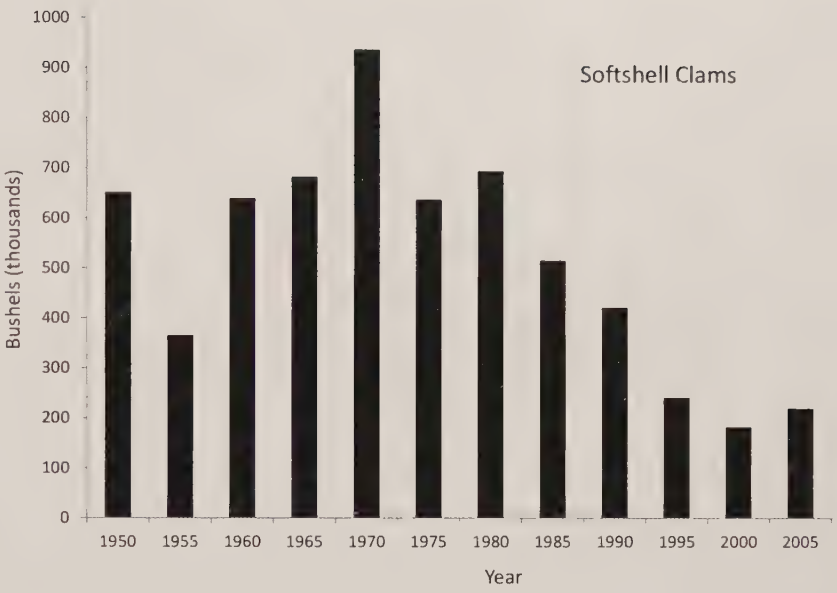

Figure 6.—Landings of softshell clams in the major production states, 1950–2005. Source: U.S. Fisheries Statistics and Fisheries of the United States.

Table 6.—Landings (bushels x 1,000)[1] of softshell clams by state, 1950-2010.[2]

Year	ME	MA	RI	NY	NJ	MD	Total
1950	458.5	116.8	38.5	2.5	34.6	0	650.9
1955	174.8	78.5	0.9	2.7	8.6	99.5	365.0
1960	138.2	56.3	0.4	11.8	3.5	428.4	639.6
1965	130.9	81.2	13.5	15.9	2.6	588.8	832.9
1970	350.6	91.4	6.7	5.7	5.4	478.6	938.4
1975	436.5	86.4	1.4	4.8	13.0	95.9	638.0
1980	378.4	132.5	3.7	6.0	25.9	148.1	694.6
1985	316.9	61.8	0.7	11.1	24.1	101.1	515.7
1990	167.6	74.4	1.3	14.2	0	164.0	421.4
1995	124.4	76.9	2.6	12.4	0	24.9	241.2
2000	152.3	0.3	1.6	13.9	0	13.0	181.1
2005	123.8	58.9	8.4	20.8	0	8.5	220.4
2010	138.0	85.0	3.2	10.0	0	2.4	238.6

[1]A bushel contains 15 lb (6.8 kg) of meat in Maine and New York, 13 lb (5.9 kg) in Massachusetts and Rhode Island, and 12 lb (5.4 kg) in New Jersey and Maryland.
[2]NMFS annual commercial landings data found in U.S. Fisheries Statistics and Fisheries of the United States.

Declines in Daily and Seasonal Harvests

A tally of the quantities of bivalves taken daily by individual fishermen over extended times can suggest whether the landings declines were actually a drop in the abundances of the bivalves. Data are available for only oysters in Maryland and bay scallops in Nantucket, but they are somewhat suspect because the data may have been collected in a year without reference to the size of the stock that year. From 1975 to 1982, the oyster catch/fisherman in Maryland averaged 14 bu of oysters/day, falling thereafter to 7 bu/day (Tarnowski[2] and undocumented data). In 1978, the seasonal harvest of bay scallops landed/fishermen license in Nantucket was 268 bu. In the 1980 Nantucket season, the seasonal catch/fishermen license was 182 bu of scallops, and in the 1990's and early 2000's it was 86 bu. These data suggest that the abundances had fallen, but the best test for determining the relative scallop abundances among years is the total landings because nearly "all"' marketable bay scallops are harvested each year. Moreover, local fishermen and shellfish constables have stated that the bivalve stocks have declined.

[2]Tarnowski, M. 2014. Maryland oyster population report—2013 Fall Survey. MDNR Publ. 17.8192014.723, 46 p.

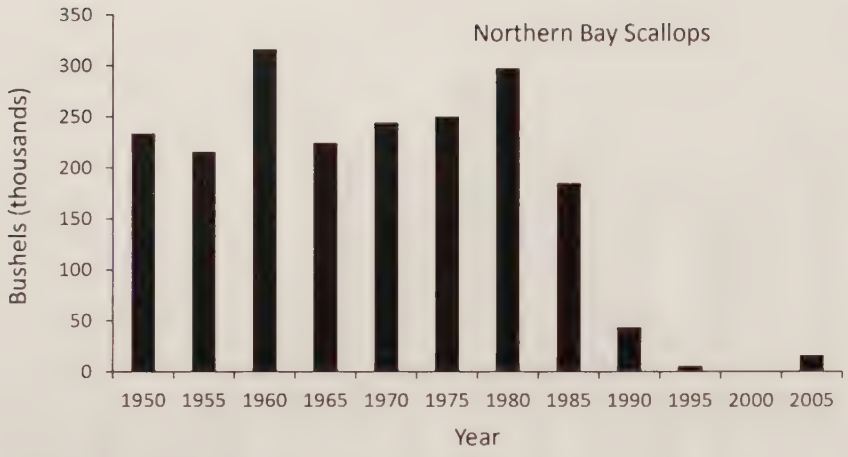

Figure 7.—Landings of bay scallops in the major production areas, 1950–2005. Source: U.S. Fisheries Statistics and Fisheries of the United States.

Table 7.—Landings (bushels) x 1000)[1] of northern bay scallops by State, 1950 to 2010.[2]

Year	MA	RI	CT	NY	Total
1950	164.3	29.8	35.2	4.5	233.8
1955	145.5	22.1	10.7	37.7	216.0
1960	154.3	0	22.9	139	316.2
1965	74.2	0.4	2.0	147.7	224.3
1970	183.5	0	0	60.8	244.3
1975	175.7	0	0	74.0	249.7
1980	225.5	0	0	71.8	297.3
1985	156.0	0	0	29.0	185.0
1990	42.4	0	0	1.8	44.2
1995	4	1.4	0	4.3	9.7
2000	0	0	0	0.6	0.6
2005	15.0	0	0	1.0	16.0
2010	21.2	0	0	0.2	21.4

[1]A bushel contains 6 pounds (2.2 kg) of bay scallop meats.
[2]NMFS annual commercial landings data found in U.S. Fisheries Statistics and Fisheries of the United States.

Factors Associated with Declines in Bivalve Landings

Bivalve abundances in the U.S. northeastern states are controlled largely by the conditions of their environments whose collective substantive elements for these species apparently remained generally stable during 1950–80. However, their conditions became altered in ways that resulted in lower abundances of the bivalves between 1980 and 2005. The altered natural factors were those affected by the North Atlantic Oscillation and higher temperatures.

We recognize that some of the temperature rise may be associated with human activities, but most of this rise was a consequence of the switch of the NAO index to its positive phase. Affected were the spawning successes of bivalves, copepod feeding on phytoplankton, most likely predation on juvenile bivalves, diseases in oysters, and declines in eelgrass. Direct human factors causing degradation to bivalve environments have been eutrophication, siltation of oyster beds, deterioration of oyster shell availability (partially from commercial harvesting actions), and hydrodynamic alterations (e.g., changes in salinity and current regimes due to inlet stabilizations) (Table 8). The strength of consumer demand has also affected commercial bivalve landings.

Natural Factors Affecting Bivalve Recruitments

University of Rhode Island (URI) researchers may have been among the first in the United States to relate changes in marine environments to the NAO, noting that after the NAO shifted to its positive index in the early 1980's waters became warmer. Populations of demersal finfishes decreased, but pelagic finfish and benthic crustaceans increased in Narragansett Bay, R.I., and nearby waters (Jeffries and Terceiro, 1985; Keller and Klein-MacPhee, 2000; Oviatt, 2004; Collie et al., 2008). They also found that abundances of zooplankton (mostly copepods) and phytoplankton changed substantially.

Zooplankton grazing on phytoplankton was continuous during the warmer winters and was responsible for a winter–spring decline in phytoplankton. The zooplankton actively fed, even reproduced, and grazed down the phytoplankton during the warmer winters. In spring and early summer, copepods continued feeding on the phytoplankton, keeping its abundance down (Keller et al., 2001; Oviatt et al., 2002; Oviatt, 2004). During any cold winters, the zooplankton were relatively inactive, and in the following spring and early summer the phytoplankton had relatively large blooms (Keller et al., 1999, 2001; Sullivan et al., 2001). Our survey results in Massachusetts show the same zooplankton pattern relating to changing abundances of copepods and ctenophores (Table 9).

The observations on zooplankton feeding on phytoplankton in winter were supported by Smayda (1990), Li and Smayda (1998), and Collie et al. (2008) who found that the phytoplankton declined substantially in Narragansett Bay even though the concentrations of nitrogen remained about the same. The potential effect on bivalves of the NAO index switch in phase to positive by modifying the composition of the phytoplankton species was explained by Smayda et al. (2004) as follows: "Climate change appears capable of modifying the baseline community of phytoplankton; as it changes in species' compositions and abundances, it affects the grazer species including the bivalves that have to adjust to it and thereby their abundances are altered."

Bivalves Failed When NAO Positive Phase Peaked in the Late 1990's

When the positive phase of the NAO index was at its peak and temperatures were very warm during 1989–95, recruitments and landings failures were documented in oysters, softshell clams, and bay scallops (Table 10). In the 12-yr period from 1994 to 2004, oyster spatfall in Virginia rivers failed while little or no sets of oyster larvae occurred. Delaware Bay (New Jersey) had little or no sets of oyster larvae from 1998 to 2003. Maryland experienced the lowest oyster harvest in 150 years during the 1993–94 season. After rebounding from Tropical Storm Agnes in the 1970's, Maryland's softshell clam landings fell during the 1980's. In the early 1990's, they fell more sharply and in 1995 and thereafter little of the commercial industry remained. Bay scallop landings declined during the 1980's, but collapsed from 1994 through 2003 to the extent that they barely existed. Their landings increased afterward.

Table 8.—Small-scale changes in various habitats have had negative effects on bivalve habitats and stocks.

On Martha's Vineyard, Mass., a severe storm broke a 1-mile-wide opening through a 3-mile bar forming the south side of Katama Bay.	Small fisheries ongoing for bay scallops, northern quahogs, and softshell clams ended because their habitats were destroyed.
On Martha's Vineyard, Mass., Sengecontacket Pond became eutrophic and the eelgrass all died,	ending the pond's ability to harbor bay scallops.
In Chatham on Cape Cod, Mass., a storm broke an opening through the Monomoy Island sand bar and destroyed softshell clams and their habitats inside the bar,	ending an active fishery.

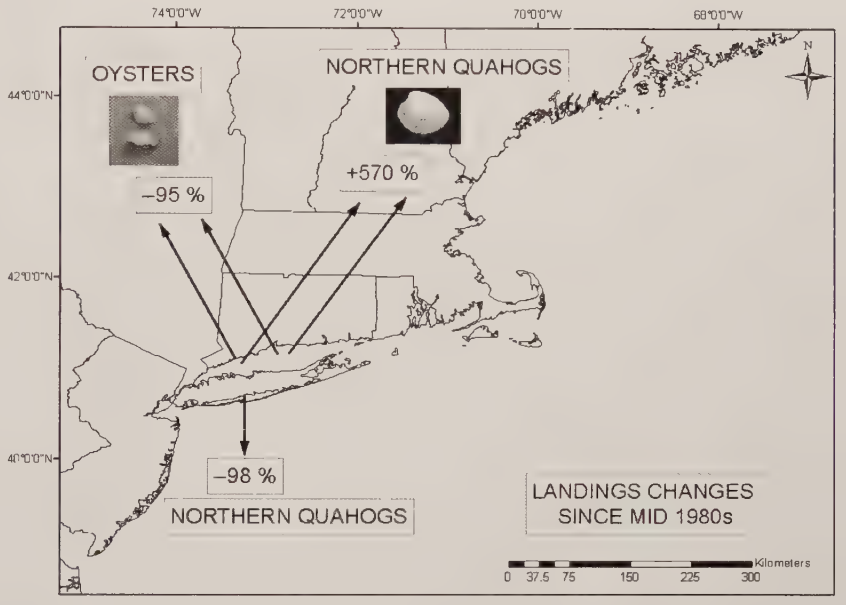

Figure 8.—Coastlines from Maine to New Jersey showing changes in landings of oysters and northern quahogs in Connecticut and New York.

Other Bivalve Decline Factors

Predation on Larvae and Juveniles

The highest bivalve mortalities undoubtedly occur in their pelagic larval stages (Rumrill, 1990). Depending upon location, their most likely predators include larval crustaceans (mostly larval shrimp and crabs), the benthic anemone, *Diadumene leucolena* (MacKenzie, 1977; Steinberg and Kennedy, 1979), ctenophores (Burrell and Van Engle, 1976; Purcell et al., 1991; McNamara et al., 2010), and certain fishes, including cyprinodonts (MacKenzie and Lind, 2013).

Laboratory observations have shown that some of these predators can consume bivalve larvae rapidly: *D. leucolena* can clear most late-stage oyster larvae in a small fish aquarium within 24 hours. *D. leucolina* may have a huge importance because its individuals often occupy much of the space on benthic bottoms in Delaware and Chesapeake Bays (MacKenzie, 1977).

Bivalves usually suffer heavy predation after they have metamorphosed and set on substrates. The predators include crustaceans, gastropods, and small fish. The various predators of oysters, quahogs, and softshell clams include mud crabs (family Xanthidae) that may be the most widespread and important predator; rock crabs; flat worms, *Stylochus* spp.; starfish, *Asterias forbesi*; at least three species of shrimps; oyster drills, *Urosalpinx cinerea* and *Eupleura caudata*; moon snails, *Euspira heros* and *Neverita duplicata*; striped killifish, *Fundulus majalis*; and mummichogs, *F. heteroclitus*.

Since the early 1950's, many studies have shown that individual predators can consume post-set juvenile bivalves rapidly, and juvenile mortality rates are usually high (Hanks, 1952; Carriker, 1957; Webster and Medford, 1961; Haskin and Tweed, 1976; Mackenzie, 1981; MacKenzie et al., 1985; Newell et al., 2000; MacKenzie and McLaughlin, 2000; Polyakov et al., 2007; MacKenzie and Lind, 2013). MacKenzie (1981) described the results of a 5-yr survey of predation and other factors that affected abundances of oysters from settlement of spat to market-sized oysters in Connecticut. White and Wilson (1996) wrote a comprehensive chapter titled, "Predators, Pests and Competitors" in the book, The Eastern Oyster *Crassostrea virginica*. Kraeuter (2001) described "Predators and Predation" in the Elsevier volume, Biology of the Hard Clam. Newell et al. (2000) described predation by flatworms on oysters in

Chesapeake Bay. Kulp et al. (2011) described how mud crabs prey heavily on oyster spat in Chesapeake Bay.

In Massachusetts, bottom predators of juvenile bay scallops are shrimps, including the sand shrimp, *Crangon septemspinosa*; Xanthid mud crabs; green crabs; and at least five species of small fishes. The grass shrimps *Paleomonetes pugio*, and zostera shrimps, *Hippolyte zostericola*, can feed on scallops when they are attached to eelgrass blades (MacKenzie and Lind, 2013). The scallop juveniles that have settled directly on the sediment bottom in areas devoid of eelgrass likely suffer huge losses from predation by sand shrimp, mud crabs, and small fishes such as gobies, *Gobiosoma bosc*; juvenile cunners, *Tautogolabrus adspersus*; and scup, *Stenotomus versicolor*, that prey on juvenile scallops of about 12 mm in height.

Long-term surveys of bivalve predators have not been done to determine the magnitudes of any changes in their abundances among years, but it has been observed that increases have taken place in blue crabs in the waters of Chesapeake Bay, U.S. southeast, and northward into New England; green crabs in Massachusetts; and crustaceans in Narragansett Bay (Oviatt, 2004; Collie et al., 2008). When the NAO index was mostly positive and temperatures were warmer after 1980, daily and seasonal feeding rates of the predators may have been higher (Table 11).

We have observed that mortality rates owing to predation are relatively low in these four bivalve species after they attain a height of perhaps 40 mm (and after their first winter) to when they are sufficiently large for commercial harvests (authors' observations). For instance, dredged samples of bivalves taken from commercial beds when the bivalves are mid- to market-sized (1–3 yr) reveal that most are alive; the samples commonly have relatively few "boxes" (empty, articulated bivalve shells). But in Connecticut, Delaware Bay, and Chesapeake Bay, where the diseases MSX and Dermo have killed many oysters after they attain mid-sizes, 2–3 cm (Ford, 1997), their "boxes" can be numerous in dredged samples from beds.

Before the late 1950's, oysters growing in the area from Chesapeake Bay through New England were generally free of diseases, at least those that caused any substantial mortalities. Since then, two parasites, MSX and Dermo, have caused huge losses in oyster populations in Delaware and Chesapeake Bays. The increase in mortalities is a primary reason why commercial oyster landings fell sharply (Andrews et al., 1962; Haskin et al., 1966; Ford and Tripp, 1996).

In subsequent years, some resistance to MSX in the oysters as a result of natural selection has occurred, and commercial oyster production has since increased (Haskin et al., 1966; Ford and Haskin, 1982; Ford and Tripp, 1996; Ford, 1997). Nevertheless, the percentage of Maryland oysters that died from the two diseases was about 10% in 1985, but it then increased to 22% in 1986, 44% in 1987, 46% in 1999, and was 58% in the extreme drought year of 2002. The mortality rate afterward fell when freshwater input to Chesapeake Bay returned to normal or above flows, and by 2003, when temperatures were cooler, mortalities were 5%–6% (Tarnowski).

Table 9.—Zooplankton collected in Cape Poge Pond, Nantucket Harbor, and four locations in Buzzards Bay, Massachusetts, 2011. The samples were collected with a towed zooplankton net (335µ mesh) for 10 min at each site.

	Cape Poge Pond		Nantucket Harbor		Buzzards Bay
Date	Zooplankton[1]	Ctenophores	Zooplankton[1]	Ctenophores	Total zooplankton[2]
June 6–7	211	0	3,020	0	4,738
June 20–21	224	0	775	0	5,019
July 5–6	13,976	0	37,520	0	2,821
July 18–19	15,672	0	11,548	0	362
August 1–2	227	30	130	present[3]	N/A
August 15–16	1	40	15	40	98

[1]This total includes copepods, and larvae of shrimp, crabs and barnacles, but not ctenophores.
[2]This total includes copepods, and larvae of shrimp, crabs and barnacles, and also ctenophores.
[3]Not counted.

Table 10.—Recruitment or landings failures of oysters, softshell clams, and bay scallops in specific locations during the mid-1990's and early 2000's. Correlations of poor recruitments or landings with the North Atlantic Oscillation in a high positive index from 1989 to 1995, followed by 2 negative index years, 1996 and 1997, and then three more positive index years, 1998-2000.

Oysters		
	Virginia	Data on oyster spatfall available from Virginia Institute of Marine Science Special Reports.[1] The data are average total spat/shell/yr from shell strings in the Piankatank, Great Wicomico, and James Rivers. 4 yr period: 1990 through 1993, 26.9 spat/shell. 12 yr period: 1994 through 2005, 5.6 spat/shell. 10 yr period: 2006 through 2015, 96.7 spat/shell.
	Delaware Bay, NJ	Data on spatfall (Powell et al., 2006). New Jersey's oyster setting stopped for 6 yr from 1998 through 2003.
Softshell clams		
	Maryland	Landings were falling during the 1990's. The landings were 310,000 bu in 1989, but they were 25,000 bu in 1995; 2,000 bu in 2000; 8,500 bu in 2005; and 1,155 bu in 2014.
Bay scallops		
	Massachusetts	Landings had been falling during the 1980's, but were 42,400 bu in 1990, 94,000 bu in 1992, and 23,000 bu in 1993. Then the landings fell sharply. In the subsequent 11 years from 1994 through 2003, the landings ranged from none to about 200 bu, then 2,200 bu in 2004. The landings afterward became higher, and in the 10 years from 2005 through 2014. They averaged 25,270 bu/yr.

[1]Supplied by M. Southworth, VIMS staff.

Table 11.—Predators that increased their feeding rates when temperatures were increased from lowest to highest temperature tested, laboratory observations. The salinities were from 26.5 to 32 ppt.

Species	Temperature range (C°)	Prey	Feeding rate increase	Source
Flatworm, *S. ellipticus*	5–21	oysters	4.3 X	(Landers and Rhodes, 1970)
Smooth drill, *U. cinerea*	15–25	oysters	3.1 X	(Manzi, 1970)
Rough drill, *E. caudata*	15–25	oysters	4.6 X	(Manzi, 1970)
Moonsnail, *Euspira* and *Naverita*	2–21	softshell clam	10.4 X	(Hanks, 1952)

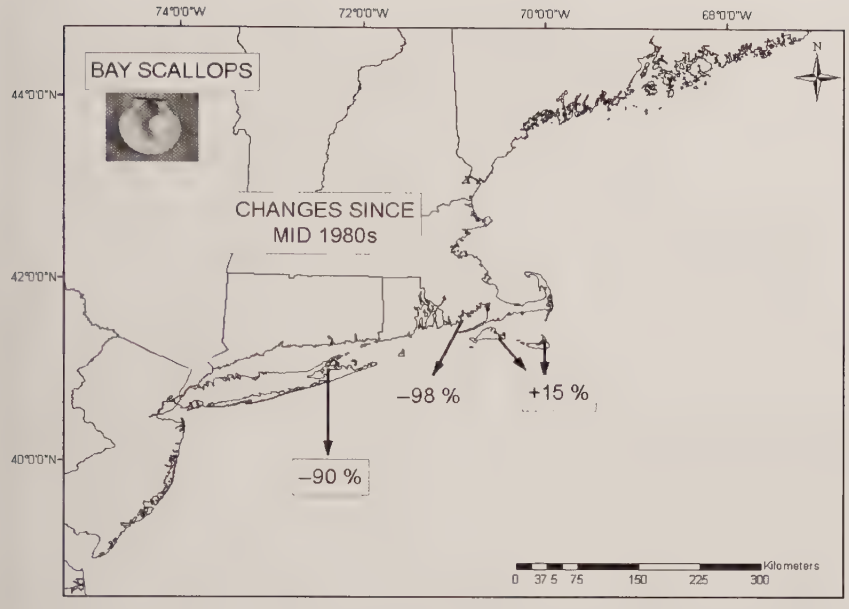

Figure 9.—Declines in bay scallop landings since mid-1980's; arrows point to major production locations.

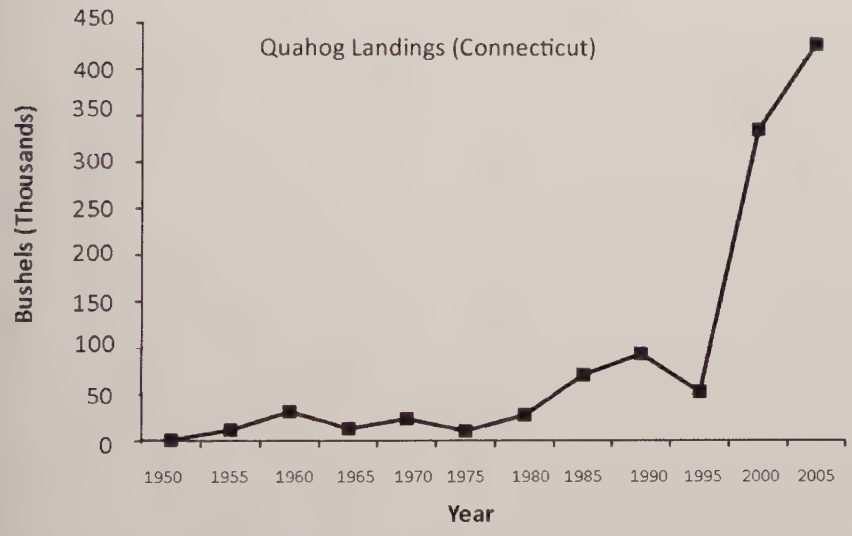

Figure 10.—Landings of quahogs in Connecticut, 1950 to 2005. Source: U.S. Fisheries Statistics and Fisheries of the United States. Note: the 2005 quahog landings were 47,000 bu

In the mid-1990's MSX killed most of the oysters in Connecticut. These oysters previously had been free of deadly diseases and oyster landings had been increasing for the previous 20 years owing to effective culturing by private oyster growers. The effects of MSX on Connecticut oysters continued into the early 2000's and its oyster landings were then limited.

QPX (Quahog Parasite Organism X) is a parasite (a fungus-like protist) of northern quahogs, first found on the Atlantic Coast of Canada in the 1950's and since then in Massachusetts. The mortalities in adult northern quahogs have been low (Anderson et al., 2003; Dove et al., 2004; Lyons et al., 2007; Smolowitz[3]; Sunila[4]).

Physical stress on bivalves from parasites may be higher in warming waters (Harvell et al., 2002). In Maryland, commercial populations of softshell clams are at the southern end of their range. Increasing temperatures and at least two diseases, disseminated neoplasia and infections of *Perkinsus chesapeaki*, may have been responsible for the steep drop in landings of this species during the 1990's from which the population has yet to recover. Populations of another commercially-important bivalve, the stout razor clam, *Tagelus plebeius*, were also found to be infected with disseminated neoplasia and *P. chesapeaki* when they suffered high mortalities in northern Chesapeake Bay in 2003 (Homer et al.[5]).

Habitat Declines

Eelgrass

Eelgrass "meadows," composed of many thin blades 4–10 mm wide and typically 20–50 cm long, form plant canopies over shallow estuarine and bay bottoms. The meadows often occupy extensive areas of some bays from Maine to North Carolina, and in the Canadian Maritimes from Nova Scotia to Quebec and Newfoundland (Fonseca and Uhrin, 2009). Eelgrass meadows can provide suitable environments for bay scallops and other molluscan species, crustaceans, fish, and other taxa. These animals are far more abundant in the meadows than in unvegetated sand bottoms nearby (Heck and Orth, 1980; Orth et al., 1984; Sogard and Able, 1991; Hanson, 2004; Fonseca and Uhrin, 2009; MacKenzie and Lind, 2013). On sand bot-

[3]Smolowitz, R. M. 2000. Roger Williams Univ., Bristol, R.I. Personal commun.

[4]Sunila, I. N.D. Report from Connecticut Department of Agriculture. Bureau of Aquaculture and Laboratory. Date: 2000.

[5]Homer, M., C. F. Dungan, and M. Tarnowski. 2001. Assessment of Chesapeake Bay commercial softshell clams, *Mya arenaria* and *Tagelius plebeius*, with emphasis on abundance and disease status. Completion Rep. to NOAA Ches. Bay Fish. Sci. Prog., NAO7NMFS4570326.

toms without eelgrass and *Gracilaria*, bay scallop larvae may find only scattered stones on which to set (Marshall, 1947).

The presence of eelgrass is important for bay scallops. When water current flows strongly, eelgrass blades lean over, come closer together, and most water overflows them (Fonseca et al., 1983; Fonseca and Cahalan, 1992). Eelgrass meadows can also dampen the effects of waves during storms on shallow bottom habitats. In their absence, storms may wash scallops into piles within shallow channels, where many die, and also fatally onto beaches (Fonseca et al., 1983; Eckman et al., 1989).

We suggest that the canopies may entrap scallop eggs and sperm during spawning in the relatively still water within the meadows, thereby increasing the likelihood of fertilization. In an absence of eelgrass, these gametes likely become scattered and fewer larvae would result.

Taylor[6] suggests that eelgrass serves to maintain scallop larvae in bays. Based upon laboratory studies in which he observed that bay scallop larvae swim upward in cool waters and downward in warm waters, he concluded that during flood tides the larvae probably swim upward into the cooler waters that enter bays through inlets from sounds outside and are carried farther into the bays and away from the inlets. About 6 h later, when the bays' waters have warmed and the ebb tides begin, the larvae descend toward the bottom to or into the eelgrass canopies and are retained in the bays. Without eelgrass, few larvae might be retained in the bays. Most areas that have lost their eelgrass have also lost their scallops.

Another important feature of the presence of eelgrass is that their blades present an attachment surface for scallop larvae, which has many times the area of the flat-bottom surface below.

[6]Taylor, R. E. 1985. The ascending and desending of larvae of bay scallops, *Argopecten irradians*, in relation to water temperature. Unpubl. manuscr. on file, P.O. Box 1652, North Falmouth, MA 02556

In Massachusetts, eelgrass canopies are fully grown by early June and are present when bay scallops spawn and their late-stage larvae are present in late-June–August. The larvae attach to the blades and then as juveniles suspended above the bottom, they are safe from large losses to bottom predators. However, some losses do occur to predation by grass shrimp, *Paleomonetes pugio*, and the shrimp, *Hippolyte zostericola*, that live in the canopies. Scallop larvae also set directly on the bottom and those likely suffer large losses from predation by sand shrimp, small Xanthid crabs, and small fishes, such as gobies, *Gobiosoma bosc*; and juvenile cunners, *Tautogolabrus adspersus*. The scallops attached to eelgrass eventually drop to the bottom after growing to a height of about 10–11 mm. By this size, they are too large for most bottom predators to consume (Belding, 1910).

Eelgrass has declined in many places (Fonseca and Uhrin, 2009). Eelgrass and bay scallops once lived together on the shallow-water bottoms adjacent to the south shore of Cape Cod in Nantucket Sound, and in Buzzards Bay, Mass.; Narragansett Bay, R.I.; Peconic Bay, Long Island, N.Y.; Barnegat Bay, N.J.; and Chincoteague and Chesapeake Bays (Orth and Moore, 1983; Fonseca and Uhrin, 2009), but both species now are much less abundant or absent in these locations. Documented causes of the eelgrass losses include high nitrogen loads and eutrophication (Fox et al., 2008; Kennish et al., 2010), shading by dense phytoplankton blooms, dark silted water, and loose algae (Oviatt et al., 2003; Kennish et al., 2013). Another cause is high temperatures as its upper temperature tolerance is about 25°C (Zimmerman et al., 1989; Bintz et al., 2003; Fonseca and Uhrin, 2009).

Setting Substrates

Availability of substrate surfaces on which ready-to-set larvae of bivalves can successfully attach and grow is a large factor that controls the recruitments of juveniles (primarily oysters and bay scallops but also quahogs and perhaps softshell clams). Historically, a huge problem for oyster populations, which create their own habitat for settling larvae, has been the decline of setting substrates. As oyster populations have declined from their formerly large expanses, increasingly less shell substrate for setting larvae has been produced or remained.

When oyster populations were large, substrate areas could be maintained by regular or occasionally large widespread sets of spat. Such sets cannot occur anymore, because when a huge spawning does take place, nearly ali the larvae perish due to a lack of substrates. On Connecticut's uncultivated beds, where salinities are about 27 ppt, few shells remain on large areas where earlier productive beds were once present. Some shells and oysters were buried by severe winds storms and any shells and stones that remain on the sand bottom surface are covered by bryozoans, barnacles, sponges, or silt, rendering them unable to receive oyster larvae. In Delaware Bay (Delaware) and Chesapeake Bay, where salinities may be 10–18 ppt, some shells are covered with so much silt that oyster larvae are prevented from setting (MacKenzie, 1983).

Visual surveys of active oyster beds (MacKenzie, 1981, 1983) in Delaware Bay (New Jersey) and Chesapeake Bay (Maryland) revealed that large bottom areas had only a partial cover of shells and live oysters. In Delaware Bay, about 30% of the bottom on some beds had too few shells to support oyster harvesting, and much of the shell material consisted of small oyster shell pieces, 10–30 mm across, that tended to lay flat on the bottom and collect too much silt to allow settlement of invertebrate larvae.

These bottoms had been dredged extensively by oystermen over the years and much original shell cover had been removed or broken into small pieces. In describing substrate loss in Delaware Bay, N.J., Powell et al. (2006) showed that when recruitment of oyster juveniles had stopped for about 6 yr (from 1998 to 2004), almost half the shell on bed surfaces was lost ow-

ing to bioerosion, breakage, and dissolution. Soniat et al. (2012b) found that whenever fishermen harvest oysters while returning blank shells to the beds, the quantity of shell removed slightly exceeds the original quantity that had been present on the beds.

Such shell losses do not occur on every type of oyster bed as was shown by a study in the James River, Virginia, by Woods et al. (2005). Most beds in this river consist of deep deposits of densely-packed oyster shells, mixed with mud, that extended as much as 4 m below the bed surface. Oyster seed was removed nearly annually from some of these beds by hand tongers from the 1870's to the 1940's. During that time, their harvesting of seed was lowering average heights of the beds by 0.47 m (Woods et al., 2005). Even as the beds were lowered, the entire surface of shells remained to provide adequate substrates for oyster larvae. Spat abundances did not decline from year to year on such beds except when silt covered them (MacKenzie, 1983).

In some locations, quahogs can be abundant in sandy substrates that have shell mixed into them to provide them cover from predation (Wells, 1957; Homer et al.[5]). MacKenzie et al. (2006) found that quahogs require an environment of densely-spaced amphipod tubes, *Ampelisca abdita*, occurring on a mud bottom to set and survive, at least in Sandy Hook Bay, N.J. The tubes presumably serve the same function as obstacles to predators, and they also stabilize the mud surface, likely a survival benefit for tiny post-set quahogs. MacKenzie and Pikanowski (2004) showed that digging quahogs with a hand rake in sand bottoms does not affect the bottom as a habitat for the setting of invertebrate juveniles, since the grain size of the bottom surface was not altered by the raking.

Softshell clams also tend to occur in higher abundances in the mud/sand mixtures containing shell (Homer et al.[5]). The hydraulic escalator dredge used in harvesting these clams in subtidal areas in Maryland may re-sort the sediments and redistribute the shell. The bottom afterward may have a surface of fine sand devoid of shell, and the altered surface forms a different setting substrate for the next generation of clam larvae. There is no documentation to assess whether such harvesting affects clam recruitment.

As mentioned above, eelgrass meadows are an important habitat for bay scallops, and their extent has declined in many locations. However, the bay scallops on Martha's Vineyard and Nantucket Harbor have made use of an alternative, the red alga, *Gracilaria* sp. (phylum Rhodophyta), which has overgrown much of the eelgrass, leaving it alive but lying close to the bottom and unavailable to the scallops. Scallop larvae set readily on *Gracilaria* and this alga is a poor habitat for the scallop predators, such as the shrimps, mud crabs, and fishes, and thus few are present. The scallops have been abundant in the areas that *Gracilaria* covers because many survive predation after setting.

In the coastal estuaries and bays from south of Cape Cod to North Carolina, the distribution of some bivalves may potentially move northward or to deeper waters when the habitat becomes warmer, similarly to the surfclams, *Spisula solidissima*, off the Delmarva coast (Weinberg, 2005). But if they attempted to occupy new habitats, their abundances might not be the same because they may encounter adverse habitat or environmental conditions, such as too few shells, hypoxic/anoxic conditions, different sediment grain sizes, different biota, and their larvae could be subjected to different water currents. Softshell clam populations in Chesapeake Bay cannot move from the warmer shallows to deeper water because dissolved oxygen concentrations are often too low. Several factors have been demonstrated to affect distributions of various invertebrates: sediments (Sanders, 1956; Snelgrove et al., 1999; Compton et al., 2009), sediments and benthic fauna (Galtsoff and Loosanoff, 1939), macroalgal assemblages (Vaz-Pinto et al., 2013), and depths and currents (Loosanoff and Nomejko, 1956).

Human Factors

Several direct human factors affect bivalve environments. These include eutrophication, unintentional removal of shells (cultch) from beds during oyster harvests (as described above), hydrodynamic alterations, and siltation of oyster beds.

In the U.S northeast, some estuaries and bay waters have been receiving large quantities of land-based nutrients (mainly nitrogen but also phosphates) and other pollutants via surface runoffs and ground waters.[7] The nutrients are delivered in streams and rivers draining urban centers, farms, and by atmospheric deposition (NRC, 2000; Boesch et al., 2001; Cloem, 2001; Howarth et al., 2002). Such waters become eutrophic to varying degrees. Productivity of animals and plants in waters depends on externally supplied nutrients (Mahoney et al.[8]), but nutrient over-enrichment and eutrophication have led to large increases in phytoplankton biomasses (Edwards et al., 2001).

The consequence has been large phytoplankton blooms, low oxygen concentrations on the deepest bottoms, especially in summer, and a general degradation in the biota of some coastal and bay waters and bottoms (Boesch et al. (2001). The nitrogen and other nutrients probably affect entire food webs as they flow through them (Nixon, 1995; Boesch et al., 2001; Rabalais, 2002).

During the mid-1950's to mid-1980's, eutrophication in Chesapeake Bay increased by at least 40% because the bay's ecosystem absorbed loads of nitrogen and phosphates that increased by about 7- and 18-fold, respectively. During this time, the human population in its watershed nearly doubled, and the use of inorganic fertilizer nearly tripled (Crossett, 2004). Little

[7]The waters include Buzzards Bay, Narragansett Bay, Great South Bay, Raritan Bay, Barnegat Bay, Chesapeake Bay, and Chincoteague Bay.

[8]Mahoney, J. B., P. S. Olsen, and D. Jeffress. 2006. Bloom history of picoplankter *Aureococcus anophagefferens* in the New Jersey Barnegat Bay–Little Egg Harbor system and Great Bay, 1995–1999. NMFS Northeast Fish. Sci. Cent. Ref. Doc. 06-08, 54 p.

scientific documentation exists on the precise effects of eutrophication and hypoxia on living resources (Boynton et al., 1996; Boesch et al., 2001; Kirby et al., 2007). Major fluctuations are common in nutrients and phytoplankton at time scales ranging from every two weeks to once a month as well as seasonally and interannually (Turner et al., 2006).

A review of eutrophication effects on bivalve abundances cannot be considered directly because the temperature has risen simultaneously with it in the same locations since the early 1980's. Kroncke et al. (1998) believe that climate variability may have a larger effect on benthic ecosystems than eutrophication and some other possible factors, but Paerl (2006) suggests it has been difficult to distinguish between these two effects. Nitrogen enrichment does lead to increases in shell growth and soft tissues in quahogs, softshell clams, and bay scallops (Carmichael et al., 2004; Wall et al., 2011, 2013). Anoxia can occur when phytoplankton blooms die in eutrophic waters, killing larvae and postset bivalves.

We cannot explain how eutrophication actually affects bivalve productivity without knowing how changes in phytoplankton species and abundances affect the bivalves. Substantial changes have been documented in the phytoplankton dynamics in Chesapeake Bay and in the lagoons along the U.S. east coast due to their eutrophication and higher temperatures: 1) the phytoplankton has shifted toward communities with abundant picoplankton and nanoplankton, and 2) the species composition changed from an assemblage consisting mainly of immobile centric diatoms to one composed of flagellated species (Harding, 1994; Bricelj and Lonsdale, 1997; Kennish, 2001; Trice et al., 2004; Wasniak and Gilbert, 2004; Kemp et al., 2005; Mahoney et al.[8]; Bricelj[9]).

In Narragansett Bay, a decrease in diatoms coincided with an increase in dinoflagellates (Smayda, 1973) and small phytoplankton species (Oviatt et al., 1989). There also have been changes in the timing, qualities, and sizes of the phytoplankton blooms (Officer et al., 1984). The food web alterations likely modify the benthic communities in bay waters considerably (Rabalais, 2002; Marcus, 2004; Smayda et al., 2004; Paerl, 2006). Bay scallops have become scarce in Buzzards Bay, Mass. This may be in part due to a shift in the bay's phytoplankton composition, which can include dense blooms of the dinoflagellate *Cochlodinium polykrikoides* that they cannot use as food (Tang and Gobler, 2009).

Eutrophication and higher temperatures (also higher salinity in Great South Bay) may have allowed the picoplankter *Aureococcus anophagefferens* to form dense blooms, leading to the decline in northern quahogs in each of the largest east coast lagoons, namely, Great South Bay, Barnegat Bay, and Chincoteague Bay (Kennish et al., 2007). The waters of the three lagoons are mostly 1–2 m deep, and flushing and circulation are limited by their small inlets. These waters once had been relatively clear, but the blooms usually have made them turbid and brown. Nuzzi and Waters (1989) have categorized them as being "bloom sensitive." Factors associated with the *A. anophagefferns* blooms are warm temperatures, still winds, and clear skies that result in high radiance.

Quahogs cannot use *A. anophagefferns* as food, and recruitments of their juveniles consequently have failed (Kennish, 2001; Bricelj and McQuarrie, 2007; Newell et al., 2009). During blooms, quahogs and bay scallops have difficulty feeding, few can spawn, and growth of their larvae is severely reduced; little reproduction of either species occurs and bay scallops usually die (Black and Kassner, 1988; Bricelj and McQuarrie, 2007; Newell et al., 2009)

After 1975, commercial landings of quahogs from the bays declined: in Great South Bay by 100% (N.Y. State Official Commercial Fishery Landings), and Barnegat Bay by 98% (NJDEP data[10]). In Chincoteague Bay, clam densities dropped by 92%.[11]

In some bays, excess nitrogen has also led to increases in biomasses of the seaweeds *Cladophora* spp., *Gracilaria* spp. (Orth and Moore, 1983; Boesch et al., 2001), and sea lettuce, *Ulva lactuca* (Tyler, 2007). Drift algae can form dense mats that smother bivalves and shade eelgrass habitats (Taylor et al., 1995: Raffaelli, 2000; Tyler, 2007; Tarnowski et al.[12]) Eelgrass remains in some areas that receive relatively low, but not high, nitrogen loads (Hauxwell et al., 2003; Fox et al., 2008).

Siltation of Substrates

Silt that accumulates on oyster beds has been a large factor that caused declines in oyster abundances. Its effects likely began during the early 1800's, when farmland was first being plowed to raise crops. Delaware and Chesapeake Bays have large watersheds on which farming has been practiced extensively. Each spring, rainwater carries silt downstream from the fields, and some falls on oyster beds where stream flows slow in velocity as they spread into the estuaries (Ingersoll, 1881, 1887; Lee, 1914; Whitney, 1994; MacKenzie, 2007). Siltation is greatest in coves where water currents are relatively low.

Recent European Observations: The NAO and Warming Temperatures

In the early 1980's, the NAO shifted to its positive index, and thus, in

[9]Bricelj, V. M. 2000. Perceptives on possible factors influencing the abundances of hard clams. *In* C. J. Schlenk (Editor), Transcript of the workshop on hard clam population priorities for the south shore of Long Island, N.Y. Sea Grant. N.Y. p. 81-88.

[10]NJDEP Division of Fish and Wildlife. Nacote Creek Research Station. Port Republic, N.J.

[11]The decline in Chincoteague Bay hard clam landings was also due to legislation banning mechanical harvesting (MD DNR Office, Annapolis, MD).

[12]Tarnowski, M., M. Homer, and R. Bussel. 1999. The re-establishment of the bay scallop in Chincoteague Bay. Final rep. NMFS, NERO, Proj. No. 95-FIG-078, Grant No. NA66FK0086, Annapolis, Md., 69 p.

winter, waters were warming in European marine habitats (Beaugrand and Reid, 2003). The temperatures rose about 0.2°–0.6°C per decade at least until about 2005–06 (MCCIP[13]). In European estuaries, the highest temperature rises also occurred in winter and spring; water temperatures were about 3°C above the earlier winter means, +1°C to +2°C above spring means; 0°C to 1.5°C during summer; and <1°C above means during autumn (Beukema, 1992; Kirby et al., 2008).

More phytoplankton appeared following cold winters (Martens, 2001; Fransz and Gieskes, 1984; van Beusekom et al., 2009) as it did in Narragansett Bay, R.I. The European scientists have not considered the feeding of pelagic copepods as a factor being responsible for low phytoplankton quantities after warm winters.

Effects on Bivalves

Along the west coast of Europe, the distribution of Baltic tellin clams, *Macoma balthica*, has moved an estimated few hundred km northward from the previous warm edge of its range. They died in the southernmost areas where mean water temperatures are about 1°C higher than they had been (Beukema et al., 2009; Jansen et al., 2007). The distribution of oysters, *Crassostrea gigas*, also shifted northward, and for the first time their larvae settled and grew on blue mussel, *Mytilus edulis*, beds in the German section of the Wadden Sea (Brandt et al., 2008).

In Europe, as is true in the U.S. northeast, Kroncke et al. (1998) have shown that interannual variability of animal abundances is a consequence of climate variability. Beukema et al. (1998), Beukema et al. (2009), and Beukema and Philipparte (2010) found that annual recruitments of juvenile bivalves can vary by two to three orders of magnitude. and they are governed by temperature rather than by the number of adults and the number of eggs they produce.

[13]MCCIP. 2010. www.mccip.org.uk/annual-reort-card/2007-2008.

Numbers of cockle and blue mussel spat usually peak after cold winters. The bivalves may have evolved a strategy designed to time their recruitments to the most optimal environmental conditions for them in the spring and early summer. The bivalves profit fully from the phytoplankton bloom in late June, then they set on the bottom and grow too large for their predators, identified as juvenile shrimps and also crabs, before these predators arrive on beds. Whenever the bivalves spawn earlier due to warm winters and thereby miss the phytoplankton bloom, their recruitments may be low (Beukema and Dekker, 2005).

Lower Recruitment

Europeans have studied bivalve recruitments on natural beds extensively. All the bivalves have been declining in recruitment, biomass, and annual abundances as the climate has been warming owing to the positive NAO index and worldwide warming (Beukema, 1993; Honkoop et al., 1998; Beukema et al., 1998; Strasser and Günther, 2001; Strasser et al., 2001; Strasser, 2002; Beukema and Dekker, 2005; Nels et al., 2006). During warm winters, the bivalves have a relatively high metabolic rate that results in large losses in their body weights. In the years when winter water temperatures were from 0°C to 3°C, overall winter weight loss in the Baltic tellin was about 15%; whereas when temperatures were from 5.5°C to 7°C, the losses ranged from 33% to 40%.

The consequence of weight loss, presumably mostly glycogen, that would have been used to develop gametes in the spring, was a smaller production of eggs and sperm in the following spring and summer. This species spawns 1.5 to 7 times more eggs after a cold winter vs. a warm winter (Beukema, 1992; Honkoop and Beukema, 1997; Honkoop and van der Meer, 1997, 1998; Beukema et al., 2009). Researchers believe, however, that this variation in egg production may translate into a minor part of the variation in bivalve recruit densities (Honkoop et al., 1998).

Juveniles Lost to Predation

Most studies of predation of European bivalves were conducted on tidal flats in the Wadden Sea, but the observations were similar to those made over wider areas in this sea (Beukema and Philippart, 2010; Dekker and Beukema, 2014). Huge losses of larvae occur when they are pelagic with additional mortalities after they set on the bottom to become constituents of benthic communities. During the first weeks of their benthic lives, mortality rates in European juvenile bivalves and some other marine invertebrates due to predation likely extend well above 90% (Grosslein and Qian, 1997; Beukema and Dekker, 2014). Strong year-classes of bivalves appear to arise only when abundances of predators are low (Reise, 1993; Beukema et al., 1998; Strasser, 2002; Beukema et al., 2009).

In the Wadden Sea, brown shrimps and green crabs are the most important predators of the bivalves. After the warm winters, shrimp abundances have been from 2 to 10 times higher than after cold winters, and the numbers of green crabs are also higher (Beukema, 1991, 1992). Green crabs, as recently-settled juveniles and as older crabs, prey heavily on small juvenile bivalves but usually kill fewer than the shrimps because they arrive later and are less abundant (van der Veer and Bergman, 1987; Beukema and Dekker, 2014). Juvenile bivalves, especially the Baltic tellin, cockle, and blue mussel, are easy prey for shrimps as soon as they settle onto bottoms and huge losses of them occur (Beukema, 1992; Reise, 1993; Pihl and Rosenberg, 1984; Pihl, 1985; Honkoop and Beukema, 1997; van der Veer et al., 1998; Caceras-Martinez and Figueras, 1997; Edwards, 1997; Dijkema, 1997; Goulletquer and Heral, 1997; Hammer, 1997; Kristensen, 1997; Seaman and Ruth, 1997; Ruano, 1997; Strasser et al., 2001; Strasser, 2002; Philippart et al., 2003; Beukema and Dekker, 2005).

In the Netherlands, Keus (1986) found during one warm season that

brown shrimps consumed 500 newly-set Baltic tellins/m^2. The bivalves can survive after they become too large, a height of at least 3 mm, to be eaten by even the largest brown shrimps.

In the Wadden Sea, the observations of factors that appear to have the most control over bivalve recruitment are summarized by Beukema and Dekker (2014). They stated that critical interactions regarding recruitments between the bivalves and their environments occur when the bivalve larvae initially settle to the bottom and begin growing, and that:

1) The stock recruitment relationship usually is negative: recruitment of juvenile bivalves bears only a little relationship to the size of the adult spawning stocks, except when such stocks become extremely low or when most substrates for larval settlement are absent.
2) Bivalve recruitments usually are successful in summers that follow cold winters, probably because abundances of the predators are low.
3) Long-term abundances of shrimp were becoming higher, and this could help to explain the declining numbers of bivalve recruitments. (The shrimp numbers did not rise everywhere in European waters (Tulp et al., 2012).)
4) There were similar relationships between recruitments and winter temperatures in the Baltic tellins, cockles, softshell clams, and blue mussels. Between-year variation in magnitude of recruitment was synchronized among these bivalves. Their numbers peaked together after cold winters and were low after warm winters.

Dekker and Beukema (2014) report that just-settled predaceous shrimps can be present simultaneously with just-settled bivalve larvae after both cold and mild winters; both arrive later after cold winters. They further state that recruitment success can be predicted at about 1 or 1.5 mo after the annual occurrence of a mass settlement of larvae, because afterward predation taking place has only minor effect on ultimate bivalve abundances.

Recent U.S. Consumer Demand for Oysters: Continuing Weak and Then a Shift to Stronger

Dedah et al., (2011) has examined why during the 1990's and early 2000's landed prices of oysters were falling somewhat and why production of oysters produced by aquaculture (hatcheries) was stagnating in the United States. The fears about eating raw oysters was lingering in potential consumers, and these were enhanced by media reports that described labels displayed on sales counters in California and other states warning people about the potential danger of eating raw oysters.

Further weakening of consumer demand for bivalves came when media reports that the waters, oysters, and other seafoods taken from U.S. state waters on the Gulf of Mexico contained dangerous amounts of bacteria, organic wastes, and oil due to the effects of two large habitat disasters: Hurricane Katrina in late August of 2005, and the Deepwater Horizon Oil Spill in April–May, 2010. Another health reason for people to avoid eating oysters and softshell clams is that their meats are commonly fried and are said to contain "hard fats" that some people prefer to avoid. During the 1990's, sales of oysters from Connecticut were slow. Its companies could not sell their entire stocks of market-sized oysters and were seeking markets in Europe with little success. In the mid-1990's, Connecticut oysters were dying from diseases and the problem of limited markets became less of an issue.

In more recent years, the marketing situation regarding oysters has changed sharply. Consumers are now eating far more oysters and most are raw on the half-shell. The implementation of rules developed by the ISSC (Interstate Shellfish Sanitation Conference) issued under strict guidelines, known as the HACCP rules (Hazzard Analysis and Critical Control Points) between January 1997 and January 2000, has meant that raw oysters have been reasonably safe for people to eat because they are maintained chilled on ice, in many cases from the time they are taken from waters on the decks of harvesting boats, transported in refrigerated trucks, and displayed in market show cases. The rules have allowed science-based testing of oyster and quahog meats for bacteria, including *Vibrio parahaemolyticus* and other pathogens. Enforcement of the rules by state public health officials has been strict. Associated with this large rise in consumption has been the increase in oyster aquaculture development (hatchery-reared seed and grow-out beds), and the increased marketing of branded oysters in raw bars and restaurants.

Overview and Assessment of Swings in Bivalve Landings

The North Atlantic Oscillation, being in a high positive index most of the time during 1980 to 2003, had strong adverse effects on the environments of commercial bivalves in the estuaries and bays of the northeastern U.S. The main effect was the warming of waters during winters. This resulted in poor recruitments of juveniles and bivalve landings falling sharply. In the Wadden Sea, the Netherlands, a series of warm winters in 1988–90 similarly led to a series of low bivalve recruitments (Beukema and Dekker, 2005). Our assessment has found that body weights of bivalves fell as their metabolic rates were relatively high but little food was available to them if they were able to feed. Then in spring and early summer, still less food was available, fewer larvae were produced, substrates for setting larvae declined, predation of juveniles likely increased, diseases of adult oysters increased, and consequently landings became extremely low. The combined landings of the bivalves fell by an estimated 85%.

An extremely poor period for bivalve recruitment occurred during the extra warm 1990's and early 2000's, and most softshell clams were killed in Maryland and New Jersey. After 2003, when the NAO index switched

to a negative or neutral phase, winters became colder and bivalve recruitment and landings increased at least for oysters in Chesapeake Bay and bay scallops in Massachusetts. Their landings would have been much higher had the substrates (clean oyster shells and eelgrass) for setting larvae been as available as they once had been.

We cannot discount the effects of spring–summer weather on bivalve recruitments. Our undocumented casual observations regarding recruitment successes have suggested that cold snaps that can occur in late spring–early summer following temperatures that were rising for a few weeks may interrupt the ripening of the bivalve gonads to the extent that recruitment suffers. In Connecticut, Prytherch (1928) had noted that poor oyster sets resulted when summer temperatures were especially cool. Another adverse factor affecting recruitments in summer is excessively cloudy weather, or when 2–4-day northeasters occur. These probably result in a temporary loss in phytoplankton and a lack of food for larvae and then a weaker recruitment for a brood of larvae. Unusually extended periods of sunny skies may also lead to poorer recruitments.

The magnitudes of bivalve seed produced vary videly among years. Loosanoff (1965, 1966) had shown that fecundity and egg production in Connecticut oysters over a 20-yr period varied somewhat by year, whereas much wider variations occurred in the magnitudes of subsequent spatfalls produced by the oysters. He concluded that survival of the larvae while growing from their straight-hinge stage to metamorphosis and attachments to substrates is extremely small and highly variable among years. Similarly to the bivalves in the Wadden Sea, the stock-recruitment relationship of the bivalves is negative in the northeastern United States. Recruitments of juvenile bivalves bear only a small relationship to the sizes of spawning stocks, except when such stocks become too small. Recruitments of groups of bivalves are affected similarly by swings in climate. The swings in their abundances are synchronous in all four species as is true for the magnitudes in bivalve abundances in the Wadden Sea. We have also observed that once each of the bivalves survived beyond its juvenile stage, perhaps to 30–40 mm, its survival to adult stages usually was relatively high.

Studies of finfish suggest that exceptionally large recruitments of marine fish also occur when the timing, species mix, and abundance of early summer blooms fully meet their needs (Beaugrand et al., 2003; Platt et al., 2003; Castonguay et al., 2008). Perhaps the same is true for the bivalves following good spawnings.

Additional types of environmental factors, some related to the NAO, caused declines in the bivalves. Our review of predator feeding rates (Table 11) in the U.S. coastal estuaries and bays also suggests that they became faster, and they could have lasted longer each year due to the higher temperatures and the longer times they remain warm. Besides, the diseases MSX and Dermo became more virulent leading to oyster mortalities increasing sharply in Chesapeake Bay, Delaware Bay, and Long Island Sound (Burreson and Ragone Calvo, 1996; Ford, 1996; Sunila et al., 1999). Blooms of "brown tides," produced by *A. anophagefferns*, that occurred mainly in the three largest lagoons (Great South Bay, Barnegat Bay, and Chincoteague Bay) have prevented survival of bivalve larvae. The partial loss of eelgrass and also some waters becoming eutrophic in Massachusetts and Long Island, N.Y., likely played a large role in the decline of bay scallops. Regarding oysters, looking past factors such as those that are related to the effects resulting from the positive NAO and large silt accumulations on substrates, that both can result in poor recruitments of oysters, we are left mainly with attributing the poor recruitments to their being harvested with dredges that have stripped shells off the bottom. Many bottoms have scattered shells, some of which are decaying or fouled, or exist as small fragments lying on sand sediments.

The oysters, quahogs, softshell clams, and bay scallops in many bays have not been noticeably overfished, certainly since the 1970's. When bivalve stocks are heavily harvested in beds in state-controlled legal seasons, sufficient numbers of adult bivalves usually will remain to potentially produce large numbers of juveniles on the beds in the following years. The residual stocks remain because by state regulations, fishermen return the undersized bivalves (the seed) that will eventually spawn to the beds. Moreover, fishermen will suspend harvesting if their daily catches become so low they cannot earn adequate money by continuing. The quantities of bivalves that remain have the capacity to produce larvae in large numbers and they could set over wide stretches of bottom if setting substrates were available.

Published and verbal statements commonly related that landings of bivalves have declined since the early 1900's because they were overfished. For example, most biologists, including Haven et al. (1978) and Hargis and Haven (1988), believed that oysters in Chesapeake Bay must have been overfished because their landings had been falling steadily. Unfortunately, no one then knew about the NAO or its effects on marine life so they could not suggest this as an alternate cause. We have dismissed overfishing of parent stocks as the overriding reason the oysters declined in abundances at various historical times. We suggest that when oysters fell in abundance over time, the cause for them actually was "habitat degradation."

Conclusions and Recommendations

Loosanoff (1965, 1966) and the literature findings we include in this paper show that environmental factors have a dominant role in controlling the magnitudes of commercial bivalve production. The rates of survival and growth to eventual market size of the great many millions of eggs spawned and fertilized vary as the climate and weather vary.

Scattered types of local summer weather affect the successes of bivalve

recruitments. During periods of calm weather when winds may be blowing gently from the south and southwest, sporadic sharp variations in temperature, wind speed and direction, extent of cloud cover, large storms and heavy rains appear to reduce recruitments. As an example, Prytherch (1928) had observed that poor oyster sets in Connecticut resulted when temperatures were extremely cool. Northeasters, that usually endure for 2-4 days, with winds that blow commonly at 20-30 knots, drive waters containing bivalve larvae in the opposite direction than the gentle winds had been drifting them. The waters that had been calm become rough, bottom materials are stirred into the water and, along with the storm's rains, decaying organic fragments are washed from shore into the water that then becomes highly turbid. A temporary loss of phytoplankton, the food for the larvae, occurs. This may be followed by a weaker recruitment to the bottom for a brood of larvae. How many larvae survive? Are survivors carried to different places where survival will be poor? Will a subsequent brood of larvae be as large and be more successful? Availability of adequate food undoubtedly is a factor with bivalve larvae and also the extent of predation that they suffer explain some of the variability in abundances of bivalve spat.

To an extent, the magnitudes of future recruitments of juvenile bivalves probably will hinge on variations in the NAO index. Their abundances may increase or at least remain stable if its index were to be negative and most winters and springs continued to be relatively cool as most were between 2003 and 2015. The recruitments will likely fall whenever the index is consistently positive.

Winter temperatures appear to be an important factor that controls abundances of many benthic macrofauna also (Oviatt, 2004; Beukema, 1992; Kroncke et al., 1998 Beukema and Dekker, 2014). Their overall species abundances in the 1950's to 1980's probably were different than they were in the 1980's to 2003. These macrofauna have been only weakly surveyed and so comparisons may be difficult to make.

Upon discovering that comparisons of the winter (December–April) status of the NAO index and finfish recruitments can be close (Dippner, 1997), Brander and Mohn (2004), and Alheit et al. (2005) in European waters, and Kimmel et al. (2009) in Chesapeake Bay, and Aburto-Oropeza et al. (2010) in California suggest that predictions about fish recruitments could be made by determining the NAO index during winters. Such tracking might also be applied to bivalves in northeastern U.S. bay waters. Since swings in the NAO indices have effects on several components of ecosystems, Kimmel et al. (2009) suggest that researchers and resource managers could examine appropriate components, such as temperature and abundances of copepods and ctenophores, in local waters to help them make forecasts. Myers (1998), though, cautions that such relationships are often not useful because the NAO and the weather can be unstable.

The effects of shrimp predation on the recruits of bivalves and other biota need more attention, following the research studies conducted by Beukema (1993) in Europe and MacKenzie and Lind (2013) in Massachusetts. We also encourage studies be undertaken to examine the effects of copepod feeding on phytoplankton and its consequences, using the Narragansett Bay studies as examples. Can we take constructive steps to improve environments for commercial bivalves to enable them to become more abundant? Oysters would become more abundant if more substrate material (shells) for their larvae was added to setting beds. Additional study could be made of the effects of overgrowth of the alga *Gracilaria* spp. over eelgrass meadows. Some curtailment of eutrophication in waters so polluted might allow the bivalve abundances to increase.

Heretofore, landing declines of bivalve mollusks usually have been ascribed to overfishing. This paper has been prepared as part of an attempt to understand the true causes of the declines. Future actions to manage these bivalves for societal benefit will be more effective as these causes become understood.

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Appendix

We believe the increases in landings of lobsters in Maine and the Canadian Maritimes occurred because predation by the cod, *Gadus morhua*, and perhaps spiny dogfish, *Squalus acanthias*, on young lobsters fell sharply. Since 1994, the cod landings have fallen sharply while the lobster landings have increased sharply there (NOAA Landings Statistics). Any changes in the abundance of the spiny dogfish cannot be estimated reliably using landings data.

Maine lobster landings have increased 5.5-times in magnitude from the early 1980's to 2011 (Fig. A1). From the early 1950's and into the 1980's, the annual landings had remained nearly steady at 18–20 million lb (mlb) (8.2–9 million kg (mkg)). They then began to rise: in 1990, the landings were 28 mlb (12.7 mkg); in 2000, 57 mlb (26 mkg); in 2005, 69 mlb (31 mkg); in 2010, 96 mlb (43.6 mkg); and in 2011, 105 mlb (47.7 mkg). The rises were due to increases in both lobster abundance and fishing effort. The numbers of fishermen are limited but the numbers of fishing licenses still increased from 5,152 in 1950 to 5,963 in 2013, while the numbers of traps increased from 430,000 in 1950 to 2,976,000 in 2013. As far as is known, the increase in landings resulted mostly from the increase in lobster abundances (authors' observ.).

Records of lobster landings from the inshore regions, from Massachusetts to Virginia, are unavailable because a substantial portion of landed lobsters are potted in deep ocean waters outside the coastal zones; the official government landings data from inshore and offshore locations are lumped together. A record of lobster landings in Long Island Sound is from only Connecticut, whose waters extend half way across the sound to meet New York waters, and from the New York–Connecticut border just east of New York City to Saybrook, Conn., an east–west distance of about 110 km. This encompasses about 70% of the distance across the Connecticut coast.

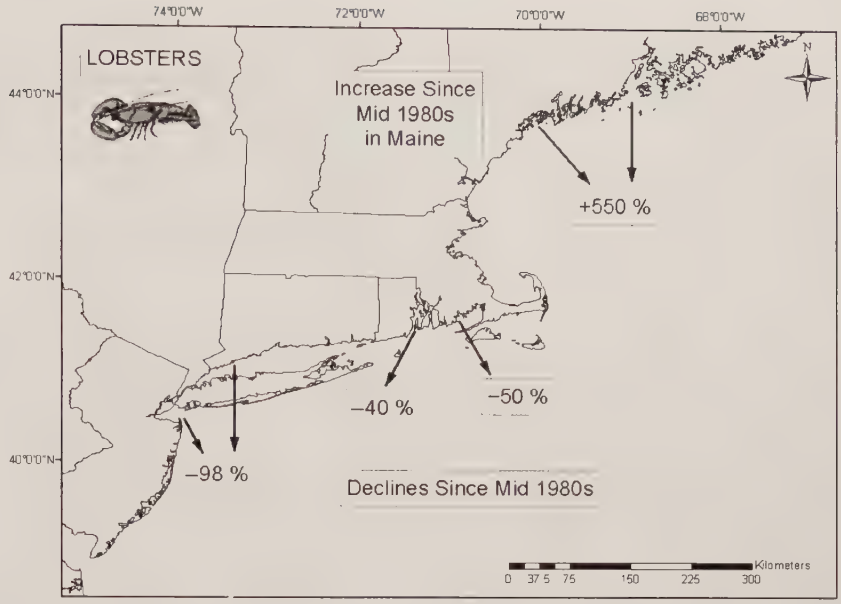

Figure A1.—Increase in lobster landings in Maine and decreases in their landings between Buzzards Bay, Mass., and New Jersey.

The Connecticut lobster landings were increasing steadily from 1,060,000 lb (482,000 kg) in 1984 to 2,584,000 lb (1,174,545 kg) in 1998. They then declined sharply because a large lobster die-off occurred in the sound in 1999. The landings totaled just 154,000 lb (70,000 kg) in 2007, down by 94%. According to Pearce and Balcom (2005), the principle reason for the lobster die-off was water temperatures rising too high in 1999: temperatures increased from an 18°–19°C range to a range of 20°–22°C. They said that the warmer waters may have accelerated an increase in abundance of the amoeba, *Neoparamoeba pemaquidensis*, that parasitizes and likely weakens lobsters, and besides low dissolved oxygen at the water-sediment interface, coupled with the release of sulfides and ammonium rising from the sediments, killed nearly all the lobsters and with them likely the rock crabs, *C. irroratus*.

Data on landings of lobsters in Raritan Bay, N.J., and upper New York Bight have never been recorded, but a decline in their abundances and landings can be estimated by examining fishing effort. This fishery began in the 1700's, and then may have continued onward. During the 1950's to early 1990's, about 28 boats with crews of 2 men each trapped lobsters daily from June to October every year. The boats each lifted about 300 pots/day (MacKenzie, 1990, 1992). During the 1990's, the fishermen found few lobsters and eventually almost none in their pots, and by the early 2000's, this fishery had ended.[1]

An epizootic lobster shell disease appeared in the inshore waters of Rhode Island and Connecticut during the late 1990's (Castro and Angell, 2000). The prevalence rates of this disease have been 10%–40% in Rhode Island waters, but there is no evidence that lobster abundance had declined due to shell disease. By 1997, though, a sharp decline in landings and population indices was recorded and it continued thereafter. No one precisely knows what factor was responsible for the lobster declines, but it is suggested that water temperature became too high (Gomez-Chiarri and Cobb, 2012).

[1]Fishermen interviews and personal observations.

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Minimizing Nordmøre Grid Bar Spaces in an Australian Penaeid Fishery

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Introduction

Concerns about penaeid-trawl discard mortality, and especially juveniles of important fish stocks, have led to various resolution strategies (Hall and Mainprize, 2005). Excluding closures, the most common approach has been to locate bycatch reduction devices (BRD) anterior to the trawl codend (Broadhurst, 2000).

One of the most effective BRD is the Nordmøre grid, which comprises separated bars (e.g., 20–100 mm) and is installed at angles of approximately 30°–48° in the extension section of trawls, with or without an anterior guiding panel and either a horizontal or triangular escape exit at the top (Isaksen et al., 1992; Broadhurst et al., 1996; Brewer et al., 1998; Silva et al., 2012). Intuitively, the performance of the Nordmøre grid should be strongly affected by the bar spaces relative to the sizes of the penaeids and unwanted bycatch. However, few studies have been published in the primary literature that test for any association between bar spacing and catches in penaeid trawls (but see Silva et al., 2012).

One penaeid-trawl fishery in which the Nordmøre grid has been successfully implemented, but for which there are no formal data assessing variations among bar spaces, occurs in estuaries in New South Wales (NSW), Australia. This fishery involves 115 small trawlers (mostly <10 m and 110 kW) diurnally targeting school prawns, *Metapenaeus macleayi* (all <25 mm carapace length; CL) mostly during the Austral summer for annual catches of 400 t per annum valued at almost AUD $3 million. A Nordmøre grid with 20 mm bar spaces was adopted by many fishermen 25 years ago and was shown to reduce total bycatch by >70% while maintaining catches of school prawns (Broadhurst et al., 1996). The 20 mm bar spacing was chosen based on school prawns being similar in size to those in European fisheries (*Pandalus borealis*) (Isaksen et al., 1992). However, the appropriateness of this spacing has never been tested. Our aim here was to assess the effects on target and bycatch species when bar spaces are reduced to a size approaching the maximum carapace thickness of the largest school prawns.

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ABSTRACT—The effects of reducing bar spaces in a generic Nordmøre grid used in an Australian penaeid-trawl fishery were investigated within an objective of maximising bycatch reduction while maintaining target catches. Compared to a conventional Nordmøre grid with 20 mm bar spaces, those with 16 and 18 mm bar spaces maintained the retained weights of school prawns, Metapenaeus macleayi, *and with no effects on size selectivity, but caught incrementally lower weights of total fish, which for the 16 mm grid was significant (mean reduced by ~26%). The results imply that Nordmøre grid bar spaces can be reduced to a size approaching the width of the largest penaeids with no commercial impacts.*

Methods

The work was done in the Clarence River (lat. 29° 27S, long. 153°12'E), NSW, Australia using one commercial double-rigged otter trawler (10 m) fishing across sand (2–20 m depth) over six days. The trawls used were identical four-seam Florida Flyers[1] (7.35 m headlines) made from 42 mm stretched mesh opening (SMO) polyethylene (PE) netting (1.2 mm diameter–Ø twisted twine) (Fig. 1a). The trawls were attached to 2.89 m sweeps and cambered otter boards (1.07 × 0.76 m; 54 kg) and had extension sections made from 41 mm SMO PE netting (1.3 mm Ø twisted twine) measuring 75 N × 100 T (Fig. 1b). Each extension section had a guiding panel (28°) terminating at the base of an inverted tombstone-shaped aluminium frame (402 × 602 mm and 10 mm square bar) secured at an angle of 45° and with an opening in the top of the codend (Fig. 1b). Conventional codends (120 × 75 B) made from square-shaped mesh (27 mm SMO and 1.3 mm Ø braided polyamide twine hung on the bar) were attached to the extension sections behind the aluminium frame (Fig. 1b).

Three grids were constructed so that they could be easily inserted into, and removed from, the two aluminum frames (Fig. 1b). All grids were made from identical materials (10 and 12 mm Ø aluminium rod bars and frames) and had the same external dimensions (400 × 600 mm) but different numbers of bars (and therefore spaces): 12 (19.69 mm; conventional grid); 13

[1]Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

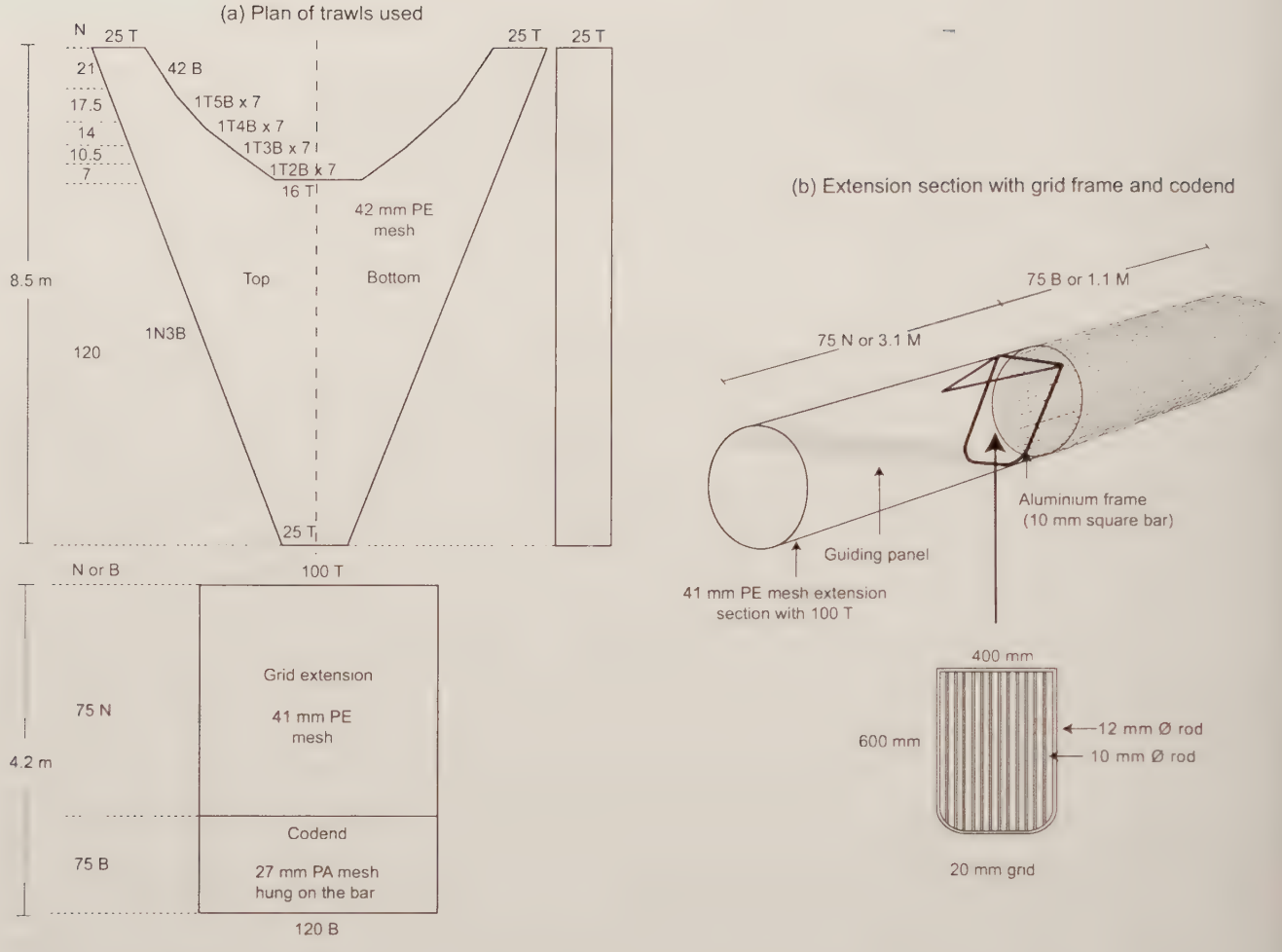

Figure 1.—The (a) trawls used and (b) extension section with grid frame (and 20 mm grid) and square-mesh codend (PE: polyethylene; PA: polyamide; Ø: diameter).

(17.57 mm); and 14 (15.73 mm) bars. These treatments were termed the 20, 18, and 16 mm grids, respectively.

The narrowest bar space (16 mm) was chosen to be slightly wider than the maximum carapace thickness of the largest school prawns, and based on established morphological relationships between CL and maximum carapace width (CW) and height (CH) derived for individuals (5–25 mm CL) in the Clarence River by Broadhurst et al. (2004). Both CW and CH were deemed important because the orientation of school prawns during passage through the grid remains unknown. Following an absence of sexual dimorphism, common regressions were calculated as CH = 0.638CL-0.766 and CW = 0.511CL-0.496; which for a 25 mm CL individual provides maximums of 15.18 and 12.28 mm, respectively (Broadhurst et al., 2004).

For every deployment (4–8 per day), the 20 mm grid was randomly allocated to one of the paired trawls and secured within the aluminum frame (using cable ties). Either the 16 or 18 mm grids were then alternately secured to the remaining trawl. The two trawls were simultaneously deployed for standard commercial durations of 60 min. The grids were then reordered as above for subsequent deployments. Over six days fishing, we completed 17 replicate paired deployments of both the 16 and 18 mm grids against the conventional 20 mm grid.

Catches were separated and the total weight of school prawns recorded. All bycatch species and approximately 500 g of school prawns were transferred to a laboratory. School prawns were counted, weighed, and a subsample (n = approximately 100) measured for CL (to the nearest 1 mm) and used to calculate the total weight and mean CL per deployment. Fish were separated by species, counted, weighed, and measured (total length; TL to the nearest 0.5 mm).

Data for the numbers and weights of catches were separately analyzed using linear mixed models (LMM's). Prior

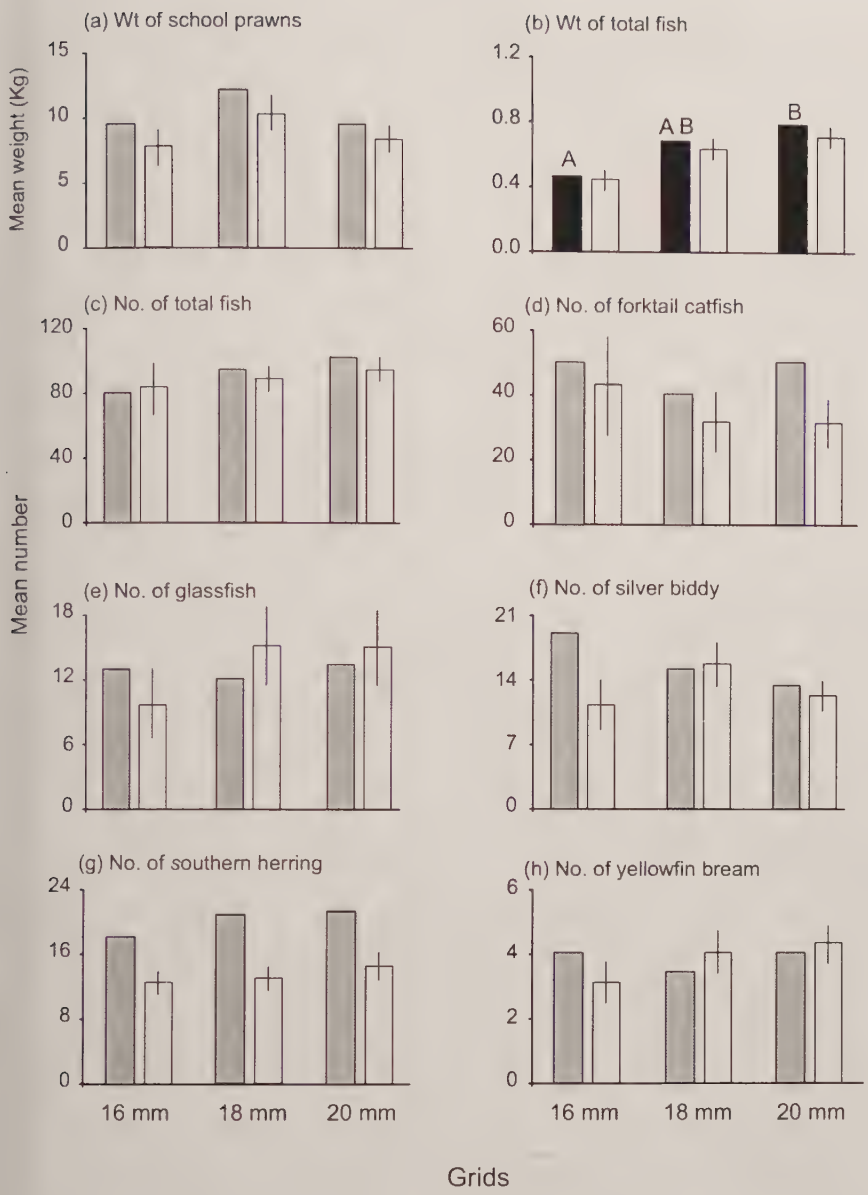

Figure 2.—Differences in predicted (shaded) and raw (±SE, white) mean catches between grids for the (a) weight of school prawns, *Metapenaeus macleayi*, (b) weights and (c) numbers of total fish, and the numbers of (d) forktail catfish, *Arius graeffei*, (e) glassfish, *Ambassis jacksoniensis* and *A. marianus*, (f) silver biddy, *Gerres subfaciatus*, (g) southern herring, *Herklotsichthys castelnaui*, and (h) yellowfin bream, *Acanthopagrus australis*. Letters above the weight of total fish indicate the direction of differences detected in false-discovery-rate pairwise comparisons for the significant fixed effect of bar spaces in linear mixed models (black histograms; $p < 0.05$).

to analyses, the numbers and weights of catches were log-transformed so that differences between bar spaces were modeled to act multiplicatively rather than additively. The mean individual mass and mean CL of school prawns per deployment were analyzed in their raw form. All models included "bar spaces" as fixed, while "trawls", "days", and the interaction between "deployments" and days were random. The significance of bar spaces was determined using a Wald F-test. Predicted mean numbers and weights were obtained by back-transforming log-predictions from the LMM's, and any significant differences were subsequently explored using the Benjamini-Hochberg-Yekutieli procedure to control the false discovery rate (FDR) (Benjamini and Yekutieli, 2001). Both the predicted and raw (±SE) means of interest were graphed.

For individual species, the proportion of the total paired catch (for each length class) retained in the trawl with the 20 mm grid was calculated. A curve was fitted to these proportions under the assumption that the grids had logistic selection. Geometric similarity was assumed so the selection curves scaled proportional to the bar spacing. Curves were fitted using maximum likelihood, with over-dispersion correction to allow for between-haul variability (Millar et al., 2004).

Results

In total, during the 34 paired tows across six days, 496 kg of school prawns (5–25 mm CL) and 44 kg of fish (or 4,447 individuals) were caught. The fish included more than 13 species, but only five species/groups were caught in sufficient quantities (>95% of the total) to permit analyses (Fig. 2).

There were no significant differences between the 16, 18, and 20 mm grids for the mean (± SE) CL's (14.35 ± 0.30, 14.40 ± 0.30, and 14.42 ± 0.29 mm CL) of school prawns or their individual mass per deployment (LMM, $P > 0.05$, Table 1, Fig. 2a). Selection curves were attempted for school prawns; but the null hypothesis of no relationship between the proportion and the CL's of school prawns was accepted for bar spaces ($P > 0.1$, Fig. 3a).

Forktail catfish, *Arius graeffei*, was the dominant bycatch (47% of the total and 5.0–10.0 cm TL), followed by glassfish, *Ambassis jacksoniensis* and *A. marianus* (16%; 4.5–10.0 cm TL), silver biddy, *Gerres subfaciatus* (15%; 3.5–15.5 cm TL), southern herring, *Herklotsichthys castelnaui*

Table 1.—Summaries of Wald-*F* statistics from linear mixed models assessing the importance of the fixed effect of Nordmøre grid "bar spaces" (conventional 20 vs 16 vs 18 mm grids) in explaining variability among catches. Excluding the mean carapace length (CL) and mass of school prawns, *Metapenaeus macleayi*, all other numbers and weights were log-transformed.

Item	Wald *F*
Wt of school prawns	2.37
Mean CL of school prawns	0.16
Mean individual mass of school prawns	0.68
Wt of total fish	3.44[1]
No. of total fish	1.80
Wt of forktail catfish, *Arius graeffei*	0.95
No. of forktail catfish	1.54
Wt of glassfish, *Ambassis jacksoniensis* and *A. marianus*	0.56
No. of glassfish	0.23
Wt of southern herring, *Herklotsichthys castelnaui*	1.21
No. of southern herring	0.38
Wt of silver biddy, *Gerres subfaciatus*	1.05
No. of silver biddy	2.14
Wt of yellowfin bream, *Acanthopagrus australis*	0.80
No. of yellowfin bream	0.63

[1]$P < 0.05$

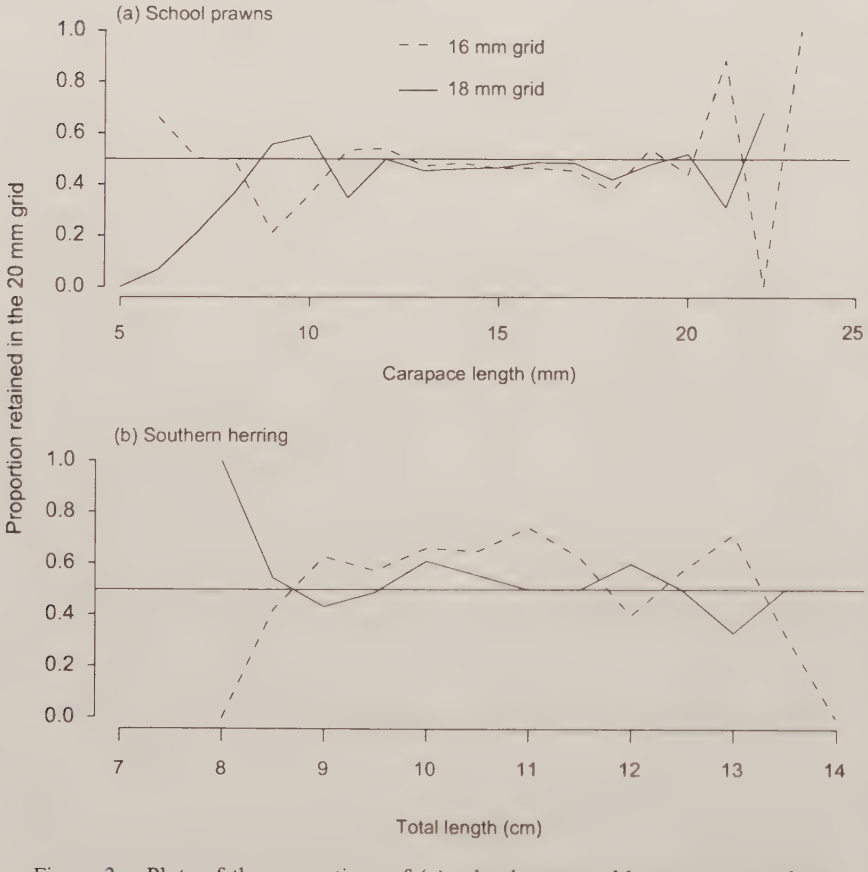

Figure 3.—Plots of the proportions of (a) school prawns, *Metapenaeus macleayi* and (b) southern herring, *Herklotsichthys castelnaui* at encountered sizes retained in the 20 mm grid during paired comparisons with the 16 and (dashed lines) 18 mm grids (solid lines).

(12%; 7.5–15.5 cm TL), and yellowfin bream, *Acanthopagrus australis* (5%; 5.5–17.5 cm TL) (Table 1, Fig. 2d–h). The LMM's detected significant differences among grids for the weight of total fish (Table 1, $P < 0.01$), with FDR's revealing that the 16 mm grid caught 26% less than the 20 mm grid ($P < 0.05$), but no differences between these grids and the 18 mm grid ($P > 0.05$, Fig. 2b). The number of total fish followed a similar mean trend among grids with up to 20% fewer in the 16 than the 20 mm grid, but this was not significant (LMM, $P > 0.05$, Table 1, Fig. 2c). Similarly, there were no significant differences in the predicted mean weights or numbers of individual species (only numbers are plotted for brevity), but some were lower in the 16 mm grid (LMM, $P > 0.05$, Table 1, Fig. 2e, f). There were no differences in size selectivity among grids for any fish (southern herring graphed as an example, $P > 0.1$, Fig. 3b).

Discussion

The data presented here contribute toward the existing literature describing technical factors affecting Nordmøre grid performances in penaeid-trawl fisheries (Broadhurst and Kennelly, 1996; Brewer et al., 1998; Silva et al., 2012; Kennelly and Broadhurst, 2014). More specifically, it is clear that bar spaces can be reduced to a size close to the CH of the largest school prawns while still consistently maintaining target catches, but with some reduction in bycatch. These observations can be discussed in terms of the species caught and their morphology, possible behaviors, and orientations at the Nordmøre grid, and then used to propose other refinements.

The maintenance of school prawn catches and the lack of any relative differences in size selection as bar spaces decreased implies that irrespective of their initial contact, all individuals were quickly orientated parallel to the angled bars (to pass through) and conceivably for many, across their width because this is their narrowest dimension. A contributing factor may have been the guiding funnel, which

directed the entire catch to the base of the grid and ensured maximum exposure to the surface. In some cases, the absence (or associated design issues) of such a guiding panel could be a contributing factor in the escape of penaeids from other grids with relatively much larger bar spaces (Broadhurst et al., 2002).

Fish also would have been similarly directed to the base of the grids, and so the significant reduction in the weight of bycatch but not numbers (although means were reduced) implies a few larger individuals passed through the escape exit of the 16 mm grid. However, although not significant, the abundant species that apparently contributed towards these reductions mostly comprised individuals with dimensions much smaller than the bar spaces. Specifically, all forktail catfish were very small (5.0–10.0 cm TL), while both species comprising glassfish have maximum TL's of approximately 7 and 10 cm, respectively and widths considerably less than 16 mm. Similarly, even a 15.5 cm TL southern herring (maximum size observed here and typically present in the river) has a maximum width < 16 mm (Broadhurst et al., 2012).

Considering the above, and the lack of any evidence of size selection, it is possible that at least some small fish (across all sizes) were able to actively swim forward after detecting the narrower 16 mm bars in the grid and out of the exit—implying a behavioral response. A contributory influence may have been the proximity (<1.2 m) of the grid to the end of the codend (Broadhurst et al., 2002). Previous studies have shown that at this distance there is significant displacement of water forward that can assist small fish to maintain position (Broadhurst et al., 1999; 2002). Any such effects might have facilitated some small fish, including glassfish and southern herring, to escape via the grid opening, and might also contribute towards the consistent passage of all small fish through the anterior section of the square-mesh codend (Broadhurst et al., 2002).

The results from this study imply that as a starting point, the bar spaces in Nordmøre grids (and perhaps other similar separating grids, such as those used to reduce catches of sea turtles) can be reduced to a size approaching the maximum CW of the targeted penaeids. Doing so will not only maintain the escape of large animals (e.g., sea turtles and elasmobranchs), but might also facilitate some behavioral escape of teleosts similar in size to the penaeids and certainly mechanical separation among those individuals that are larger (often encountered at different areas and times; Broadhurst et al., 1996). The latter is an important consideration because ideally, wherever possible, a single BRD would fulfill species-selectivity requirements, and especially for small-scale fisheries with multi-trawl configurations that generally preclude incorporating complex BRD combinations. Such work warrants ongoing attention, because despite historical efforts, bycatch in many fisheries remains a global concern that still requires applied solutions (Hall and Mainprize, 2005).

Acknowledgments

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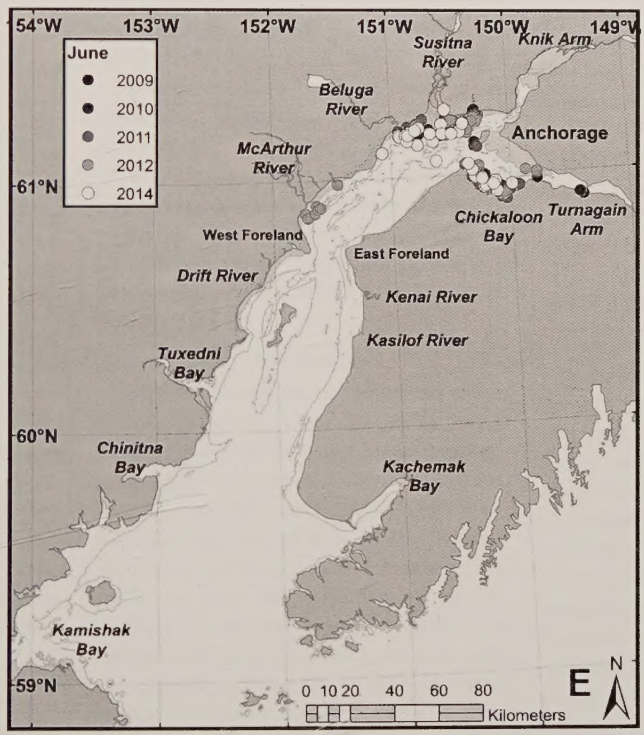
Errata

Shelden, Kim E. W., Kimberly T. Goetz, David J. Rugh, Donald G. Calkins, Barbara A. Mahoney, and Roderick C. Hobbs. 2015. Spatio-temporal Changes in Beluga Whale, *Delphinapterus leucas*, Distribution: Results from Aerial Surveys (1977–2014), Opportunistic Sightings (1975–2014), and Satellite Tagging (1999–2003) in Cook Inlet, Alaska. Marine Fisheries Review 77(2):1–31.

On page 14, Figure 5E should have shown the beluga whale group sighting locations for 2009–14. The figure has been corrected in the online version.



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Manuscripts must be double-spaced throughout, and a complete manuscript normally includes a title page, a short abstract, text, literature citations, tables, figure legends, footnotes, and the figures. The title page should carry the title and the name, department, institution or other affiliation, and complete address (plus current address if different) of the author(s). An "Acknowledgments" section, if needed, may be placed at the end of the text. Use of appendices is discouraged.

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The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be spelled out the first time they are mentioned. The scientific names of species must be written out the first time they are mentioned; subsequent mention of scientific names may be abbreviated. Follow the U.S. Government Printing Office Style Manual (2008 ed.) and the Scientific Style and Format: the CSE Manual for Authors, Editors, and Publishers (2014, 8th ed.) published by the Council of Science Editors.for editorial style, and the most current issue of the American Fisheries Society's Common and Scientific Names of Fishes from the United States and Canada for fish nomenclature. Only journal titles, scientific names (genera and species), and vessel names should be italicized. Dates should be written as follows: 11 November 2013. Measurements should be expressed in metric units, e.g., metric tons as (t); other equivalent units may also be listed in parenthesis. Common abbreviations and symbols such as mm, m, g. ml, mg, and °C (without periods) may be used with numerals. The numeral one (1) should be typed as a one, not as a lower-case el (l). Write out the numbers zero through nine unless they form part of measurement units (e.g., nine fish but 9 mm).

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